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Soil respiration around termite mounds in African semi-arid savanna

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Tiivistelmä – Referat – Abstract

Maaperä on tärkeä hiilen varasto ja maaperän ja ilmakehän välinen hiilidioksidin vuo on toiseksi suurin hiilivuo ekosysteemien ja ilmakehän välillä. Maaperän respiraation määriin on todettu aikaisemmissa tutkimuksissa vaikuttavan erityisesti maaperän kosteus ja lämpötila, mutta myös maaperän makrofaunan aktiivisuus. Afrikan puolikuivilla savanneilla näitä tekijöitä säätelee kausittainen vaihtelu. Kekoja rakentavia termiittejä on runsaasti näillä savanneilla, ja ne vaikuttavat hiilen kierron lisäksi maaperän ominaisuuksiin rakentaessaan kekoja ja etsiessään ravintoa niiden ulkopuolelta. Kekojen kaasunvaihto ja lämmönsiirto on monimutkainen ilmiö, joka vaihtelee keon arkkitehtuurin ja ympäristömuuttujien mukaan. Kekojen sisäinen tuuletus tuo termiittien ja niiden pesän aineenvaihdunnassa syntyvää hiilidioksidia kekojen ulkopuolelle. Termiittien hiilidioksidipäästöjä, etenkin niiden kekojen ulkopuolella, tulisi tutkia niiden osuuden selvittämiseksi savannien maaperän kokonaisrespiraatiosta.

Termiittikekoja ympäröivän maaperän respiraation ymmärtämiseksi respiraation määriä mitattiin Tsavon ekosysteemissä Etelä-Keniassa kahden sieniviljelijätermiittilajin *Macrotermes michaelseni* ja *Macrotermes subhyalinus* kekojen ympäriltä käyttämällä suljetun staattisen kammion menetelmää. Mittaukset tehtiin kolmen oletetun sadekauden aikana, marraskuussa 2016, huhtikuussa 2017 ja joulukuussa 2017. Tutkimuksessa yritettiin määrittää, tulivatko hiilidioksidipäästöt maaperästä vai termiiteistä. Myös vallitsevan tuulensuunnan vaikutusta tutkittiin, jotta ymmärrettäisiin paremmin kekojen sisäisen tuuletuksen roolia. Myös maaperän kosteutta, maaperän lämpötilaa ja sademääriä mitattiin ja niiden vaikutusta respiraatioon tutkittiin.

Tulokset osoittivat, että vain yhtä tiettyä syytä maaperän respiraation muutoksiin kekojen ympärillä on vaikea löytää. Suurin osa vaihtelusta mittauskausien ja mittausalueiden välisissä eroissa selittyi maaperän kosteuden vaihtelulla. Myös vallitsevalla tuulen suunnalla havaittiin olevan vaikutusta maaperän respiraation muutoksiin. Maaperän respiraatio oli suurinta kekojen läheisyydessä, joten termiittien aktiivisuuden tai niiden maaperän ominaisuuksiin aiheuttamien muutosten oletetaan olevan vaikuttava tekijä. Erityisesti vähäisen aineiston määrän takia tutkimusaiheen epävarmuustekijöitä tulisi tutkia lisää.

Avainsanat – Nyckelord – Keywords

CO_2 - *Macrotermes michaelseni* - *Macrotermes subhyalinus* – Kenia – Taita

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Tiivistelmä – Referat – Abstract

Soils are important stocks of carbon and the soil-atmosphere CO_2 flux is the second largest carbon flux between ecosystems and the atmosphere. Soil respiration is in previous studies considered to be mostly controlled by soil moisture and temperature, but also the activity of soil macrofauna. In African semi-arid savannas these parameters are controlled by seasonality. Mound-building termites are abundant in these savannas and in addition to the carbon cycle, they affect soil properties when building mounds and foraging outside them. Gas exchange and heat transfer in mounds is a complex phenomenon that varies depending on mound architecture and environment variables. Mound ventilation brings the CO_2 generated in termite and their nest metabolism outside the mounds. CO_2 emissions of termites, especially outside their mounds, should be studied to clarify their impact on the savanna soil respiration.

In attempt to understand soil respiration around termite mounds, soil respiration rates was measured from surrounding area of six mounds of fungus-growing termite species *Macrotermes michaelseni* and *Macrotermes subhyalinus* using closed static chamber method in Tsavo ecosystem, southern Kenya. Measurements were made during the three assumed rainy seasons, in November 2016, April 2017, and December 2017. Research focused whether CO_2 emissions come from the soil or from termites. The effect of prevailing wind was also studied to understand the role of mound ventilation better. Soil moisture, soil temperature, and the amount of rainfall were also measured and their effect on respiration was studied.

The results show that a single reason for the changes in soil respiration rates around termite mounds is difficult to find. Most of the variation between measurement sites and measurement periods were due to changes in soil moisture. Prevailing wind direction was also found to be possible reason for changes in soil respiration rates. Soil respiration rates were higher near the mounds, so termite activity or changes in soil properties caused by them are assumed to be a contributing factor. Due to limited amount of data, many of the uncertainties on the subject should be further researched.

Avainsanat – Nyckelord – Keywords

CO_2 - *Macrotermes michaelseni* - *Macrotermes subhyalinus* – Kenya – Taita

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1 INTRODUCTION

Soil is defined as a mixture of dead organic matter, air, water, and weathered rock that supports plant growth (Yiqi & Zhou 2010). Globally soils are also important stocks of carbon. The annual CO_2 flux from soils to atmosphere is estimated to be 75–80 Pg C yr^{-1} (Schlesinger 1977; Raich & Potter 1995), which makes it second largest carbon flux between ecosystems and the atmosphere. CO_2 plays a significant role in the carbon cycle as an atmospheric greenhouse gas, and the increase in its amounts in the atmosphere has the effect of raising the surface temperatures of the Earth.

Savannas cover about 20% of the planet's land area (Shorrocks & Bates 2015) and they are important and complex ecosystems. The most important characteristics in the African arid and semi-arid savannas is the seasonality of the rainfall with the movement of the Intertropical Convergence Zone, ITCZ (Niemelä 2011). In savannas, termites are main decomposers of soil organic matter and play a major role in carbon cycling ((Holt & Lepage 2000). The number of termites is assumed to be an indicator of a healthy ecosystem. In southern Kenyan savannas, the fungus-growing termites *Macrotermes subhyalinus* and *Macrotermes michaelseni* are considered to be the two dominant termite species. Termites affect the carbon cycle not only due to decomposition but also due to CO_2 emissions from their metabolism (Noirot & Darlington 2000; Konaté et al. 2003). Termites are also known to produce significant amounts of methane (CH_4), so their role as emitters of greenhouse gases should be further studied at global level.

Soil moisture and soil temperature are considered to be two dominant drivers controlling soil respiration, especially in dry ecosystems (Singh & Gupta 1977; Conant et al. 2004). Soil macrofauna, including termites has also a major role in releasing CO_2. They also affect their environment different ways: termites build complex mounds for their colonies and while building they modify soil properties near the mounds and thus act as ecosystem engineers (Holt & Lepage 2000; Dangerfield et al. 1998). Termite mounds are effectively ventilated with diffusivity trough their porous surface or with the help of wind (Ocko et al. 2017). This ventilation may also bring CO_2 generated in the nest outside the mound through underground foraging tunnels.

The idea of the study is to examine the activity of termites outside the mounds as they forage and outline whether CO_2 emissions come from the soil or termites. The effect of prevailing wind direction and ventilation of termite mounds on soil respiration was also considered. In addition to these, the effect of various environmental parameters was investigated, and an attempt was made to form an overall picture of the area surrounding the mound.

The study aims to answer three research questions:

1. Does the activity of termites affect soil respiration around the mound?
2. Does the prevailing wind direction affect soil respiration around the mound?
3. How other parameters affect soil respiration around the mound?

2 THEORETICAL BACKROUND

Due to the relevance to current climate change, research and number of papers published about soil respiration as part of global carbon cycle are increasing rapidly. One of the first scientist to make *in situ* measurements of soil respiration rates with the static closed chamber method was Swedish botanist Henrik G. Lundegårdh in 1927 for his study about parameters affecting crop growth. The measurement method has since been developed and used a lot in research about the topic in various environmental conditions. Since 1970s the driver in soil respiration research has been globally changing climate, because it started to become evident that the anthropogenic emissions of CO_2 have resulted an increase in the greenhouse effect and hence increased the surface temperature of the Earth. Research about soil respiration has also become a very important part of IPCC reports and its role is still increasing.

Savannas of the world have been long studied, for example Germans have been studying African savannas since the 19th century (Niemelä 2011). Nowadays savannas and their ecosystems are widely studied since they are particularly vulnerable under quickly changing climate and the droughts caused by it. Soil respiration under various savanna conditions has been studied mostly in Africa, Australia and South America. Epule's study from 2015 reveals that in Africa there has been at least 62 published studies about soil respiration and 7 of them in savannas, and that the number of papers increased from 4 to 62 in just four years (2010–2014), and continues to increase as well.

Termites, including fungus-growing termite (Macrotermitinae) species *Macrotermes michaelseni* and *Macrotermes subhyalinus* have been under a lot of research globally. In Kenya, they have been studied by for example Arshad (1982), Darlington (e.g. 1982; 1987; 1990; 1997) and Lepage (1976) in various research. Zimmerman estimated in 1982 that termites may emit large quantities of methane (CH_4) and carbon dioxide (CO_2) into the atmosphere. Those estimations turned out to be exaggerated, but it still sparked a number of other similar studies.

There have been estimations about the role of termites to atmospheric gas emissions also outside their mounds (Jones 1990) but the research about topic have been marginal. At least Holt (1987) in northern

Australia, Khalil et al. (1990) in southern Australia, Konaté et al. (2003) in Ivory Coast, West Africa, and Brümmer et al. (2009) in Burkina Faso, West Africa have been studying respiration from termite mounds and the soil around them but have not been combining or comparing results. Most of the studies made about the subject so far measured emissions by covering only the mound and ignoring the surrounding network of subterranean passages through which respiration products pass and so ignoring the potential respiration of the entire mound (Jones 1990).

2.1 Savannas

Savannas (figure 1) are tropical ecosystems that occur within 25° of the equator (Olson et al. 2001) and cover almost 20 % of the Earth's surface (Shorrocks & Bates 2015). They are usually classified as grasslands, with scattered bushes and trees that are located between the equatorial forests and the mid-latitude deserts (Scholes & Walker 2004). Key climatic characteristics in African savannas are a large amount of received solar radiation, a change of wind direction with the movement of the Intertropical Convergence Zone (ITCZ) and rainfall that occurs only during certain seasons. Rainfall variability and intensity are the key attributes in savanna climate (Bellamy & Perrault 2013) and their uncertainty and exceptions affect water availability and therefore cause droughts. The surface water balance is dominated mostly by evapotranspiration and infiltration (Turner 2006).

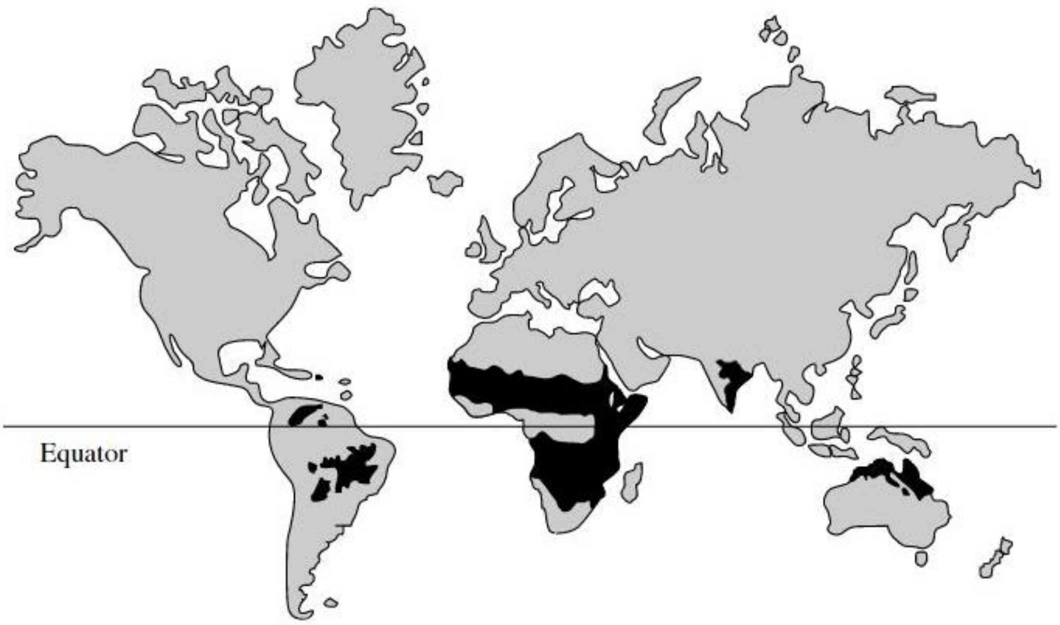

Figure 1: World distribution of the savanna biome (Shorrocks & Bates 2015). The largest area of savanna (15.1 million km^2) is in Africa, where it covers almost 50 % of the total land area (Grace et al. 2006).

Due to their favorable circumstances (temperature and precipitation) the savannas account for about 30 % of the global primary production of all terrestrial vegetation (Grace et al. 2006). Also, the decomposition rate of litter is rapid. In African savannas vegetation biomass is abundant and its changes have a clear impact on the biomass of herbivores and carnivores (Shorrocks & Bates 2015). The flora and fauna of the African savannas are unique, the best-known feature of the fauna is the diversity and biomass of large mammals and megaherbivores, e.g. elephants, so their cycles cannot be compared to the savanna ecosystems on other continents (Scholes & Walker 2004; Niemelä 2011). Elephants tend to push over and damage trees as they eat, and their destructive habits transform woody vegetation into grasslands (Haynes 2012). Due to the land cover change termites disappear from the area because there is not enough food for them, which was also observed in the area of this study.

2.1.1 Arid and semi-arid savannas

Savannas can be classified by their average rainfall. In Kenya, savanna and grassland ecosystems are typically classified to be arid or semi-arid and is mostly *Acacia–Commiphora* savanna (Shorrocks & Bates 2015). Tsavo ecosystem where the measurements were made is mostly semi-arid. Arid and semi-arid savannas are characterized by two rainy seasons due to the ITCZ movement (Niemelä 2011). Rainfall is typically 250–650 mm y^{-1} and the annual rainfall is equal to evapotranspiration, so most of the rainfall evaporates. Rainfall exceeds evapotranspiration usually during summer and vice versa in winter, so savanna soils act as a net storage of water during summer season (Turner 2006). These storages are used by plants and animals during drier seasons. When storage runs out, production of above-ground biomass declines and living biomass dies and dries. This dry and dead vegetation provides significant source of water for herbivores in arid and semi-arid savannas. Grass production in these areas is positively related to rainfall (Abbadie et al. 2006) and trees tend to be deciduous (Shorrocks & Bates 2015).

The soils of arid and semi-arid savannas are base-rich, the parent material is usually basic igneous rock, and upper soils are fine sandy loams with high bulk densities, poor moisture content and nutrient deficiencies. They also tend to be highly erodible due to high rates of infiltration (Bellamy & Perrault 2013). Savanna soil can thus be divided to sandy, infertile uplands and clayey, more fertile bottomlands, that are mostly characterized by water movement (Scholes & Walker 2004).

2.1.2 Seasonality

During the course of a year, as the Earth orbits the sun with its axis slightly tilted, the sun changes its position in the sky and produces the changing seasons (Shorrocks & Bates 2015). During the winter solstice, the sun is on the Tropic of Capricorn (23.45°S) and during the summer solstice it is on the Tropic of Cancer (23.45°N). In spring and autumn, during equinoxes, it is overhead at the equator. This location of the sun is called thermal equator, a zone of seasonal maximum temperature and it is directly related to solar heating (Barry & Chorley 2009). Thermal equator moves north and south across the equator twice a year and this results movement of air masses over Africa. The intertropical convergence zone (ITCZ) is formed due to this movement. The ascending air, heated by intense solar radiation, is cooled by expansion resulting from reduced pressure, causing saturation, condensation, cloud formation and rain (Shorrocks & Bates 2015). This dry air moves towards the poles, descends as it cools and so forms a subtropical high-pressure region. Wind from these emerging high-pressure regions blows towards the low pressure of the ITCZ. These winds are called trade winds and they always blow from the east due to the direction of rotation of the Earth.

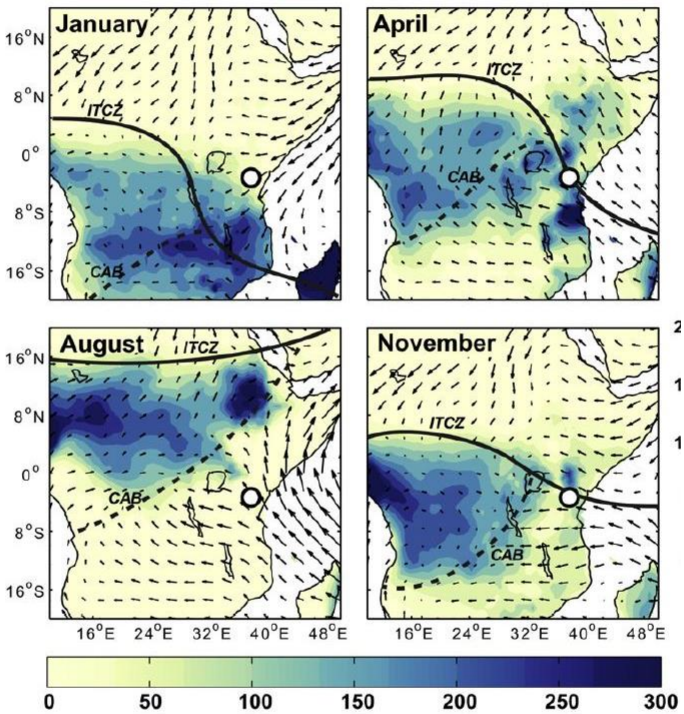

Figure 2: Seasonality of the ITCZ, precipitation rates (mm/month) and prevailing wind directions (Tierney et al. 2011). White dot represents Lake Chala, located about 50 km from measurement sites in this study.

The ITCZ does not move in a straight line to the north and south over Africa but bends in an east-west direction, adapting to Congo Air Boundary. This bending distorts the moisture gradient so that

East Africa is relatively dry compared to the rest of the continent (Shorrocks & Bates 2015). The ITCZ has been assumed to be a significant factor on rainfall in Africa and the cycle of the rainfall seasons is generally associated with its seasonal north to south movement (Nicholson 2018). As the ITCZ and so trade winds move, the prevailing wind direction changes. Figure 2 shows how in January winds are blowing from the northeast and from the southeast in April. By changing direction these prevailing atmospheric winds affect local winds and seasonal weather in East African savannas.

2.2 Soil carbon cycle

The biosphere gets its energy from solar radiation, which is converted into chemical energy through photosynthesis (Archer 2010). This reaction converts atmospheric CO_2 into a form used by plants and other autotrophic organisms. In addition to the incoming radiation, the intensity of photosynthesis is also affected by the air temperature, the availability of water and nutrients and the plant leaf area. Carbon is stored in the structure of plants and eventually ends up in the soil as dead plant material and litter decay. Some of this stored carbon returns to the atmosphere through respiration processes as CO_2. This carbon cycling can be described by the equation:

$$NEE = ER - GPP \tag{1}$$

where GPP is gross primary production, total fixation of energy by photosynthesis and ER is ecosystem respiration. NEE, net ecosystem exchange can be calculated as the difference between these. In soils NEE can be described as net balance of all carbon fluxes entering and leaving the soil over time.

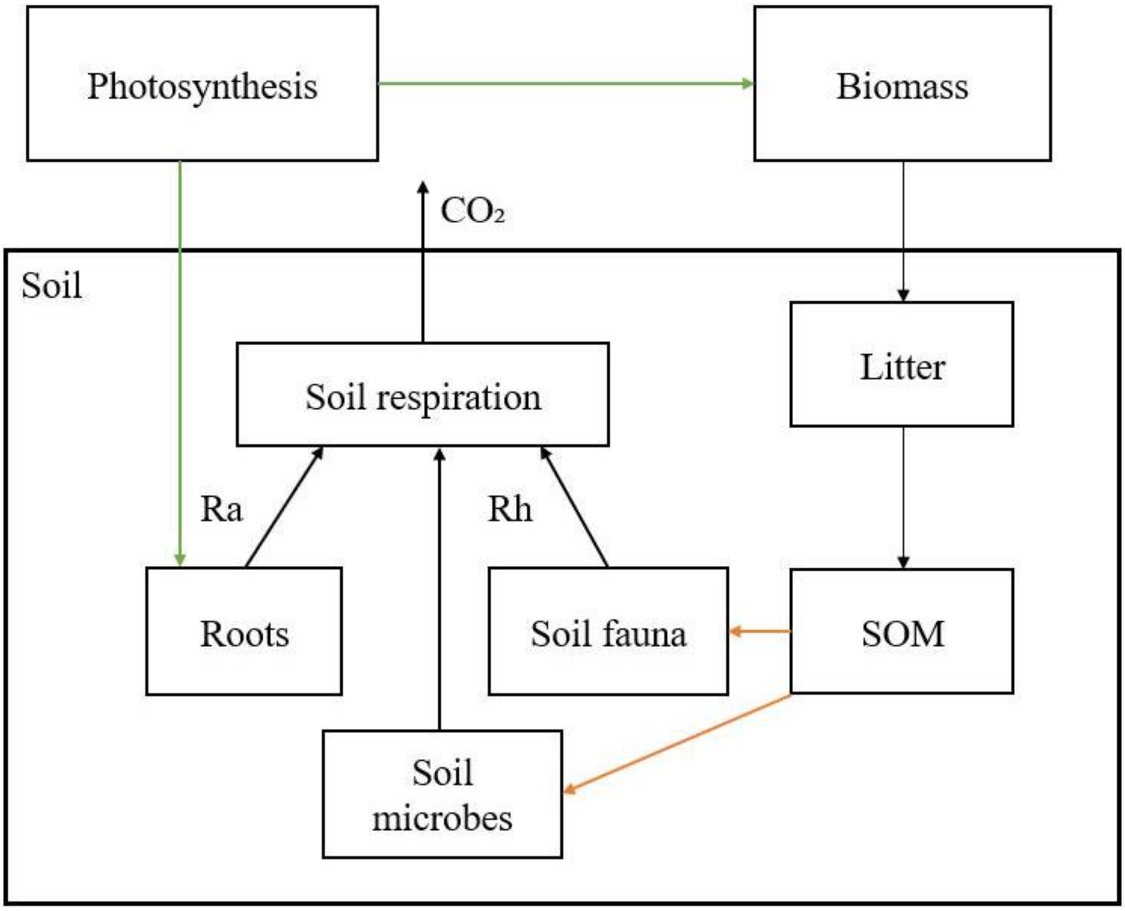

Figure 3: Basic concept model of soil carbon dynamics based on Kutch et al. 2009. Orange lines represent decomposition by soil organisms and green lines photosynthesis. Rh means heterotrophic respiration and Ra autotrophic respiration.

Soil carbon stocks are large, globally they have a carbon pool twice as large as the atmospheric pool of carbon (Schlesinger 1977). Inter-annual changes in soil carbon stocks are small compared to the total carbon stored in soils (Kutch et al. 2009). Carbon circulates between the soil and the atmosphere and about 8–10 % of CO_2 in atmosphere originates from the soil (Epule 2015). In addition to the atmosphere, the carbon cycle is also linked to the vegetation, other living organisms, and the water cycle. In savanna ecosystems carbon fluxes are tightly coupled to the seasonal patterns of rainfall and the changes in soil water content.

Carbon turnover in terrestrial ecosystems is mostly linked to biochemical reactions of three types of organisms. Primary biomass is produced by autotrophic organisms, mainly plants and their biomass is transformed by herbivores and other consumers into secondary biomass. Eventually nonliving biomass is mineralized by decomposers to CO_2 (Bird et al. 2001). Mineralization means the decomposition of chemical compounds in organic matter so that the nutrients are available to plants, for example soil organic carbon is mineralized to CO_2. Soil respiration rates are related to soil mineralization rates. Biomass entering the soil is subject to biological decay by various types of soil micro-organisms including soil fauna of different sizes (e.g. termites), bacteria and fungi (Rodeghiero et al. 2009). Soil organic matter (SOM) generally refers to the nonliving organic material within the soil. It accumulates from above-ground litter including woody tissues, leaves and dead grasses and below-ground inputs, such as dead roots and their associates. Environmental factors such as temperature, radiation, and the availability of water influence directly or indirectly the decay of biomass.

2.2.1 Soil respiration

Physiologically respiration is a series of metabolic processes that break down organic molecules to liberate energy, water, and CO_2 in a cell (Yiqi & Zhou 2010). Soil respiration is the total CO_2 production by all organisms and plant parts in soil. It includes root respiration, microbial decomposition of SOM and soil fauna respiration. Soil respiration means that the living biomass of soil respires CO_2, while soil organisms gain energy from catabolizing organic matter to support life.

Soil respiration can be divided into autotrophic respiration produced by metabolic activity of roots and their associated rhizosphere (mycorrhizae and rhizosphere bacteria) and heterotrophic respiration from soil organisms that decompose SOM (Makhado & Scholes 2011; Thomas 2012). Lundegårdh (1927) compared CO_2 production from bare soil and a similar soil covered with oats and reported that root respiration accounts for about 30 % of the total soil respiration. Nowadays the share of root respiration is believed to be approximately half of the total soil respiration (Yiqi & Zhou 2010). Raich and Schlesinger (1992), in turn, estimated that heterotrophic respiration covers 50–70 % of total respiration. The distribution of soil respiration components is still under research.

CO_2 produced in soil transfers through soil profiles to the soil surface and is released into the air by diffusion and air turbulence (Yiqi & Zhou 2010). The estimated annual flux of CO_2 from soils to the atmosphere is estimated to be 75–80 Pg C yr^{-1} (Schlesinger 1977; Raich & Potter 1995) which makes it second largest carbon flux between ecosystems and atmosphere. Even small changes in the magnitude of soil respiration could significantly intensify, or mitigate, current atmospheric increases of CO_2, with potential feedbacks to climate change (Raich & Schlesinger 1992).

2.2.2 Parameters affecting soil respiration

Soil chemical, physical and eco-physiological properties affect the rates of soil respiration. Soil chemical properties are mostly determined by their parent material, climate, vegetation, and activities of soil fauna (Holt & Lepage 2000). Soil physical properties are linked to decomposition and nutrient cycling because of the soil moisture (Scholes et al. 1994). Soil physical properties such as nutrients, porosity, and texture as well as the vegetation, topography and climate of the region are part of the parameters affecting respiration. Several research proves that soil respiration is mostly controlled by soil temperature and soil moisture, directly or indirectly (e.g. Singh & Gupta 1977).

Soil moisture affects soil respiration especially in arid or semi-arid areas (Conant et al. 2004). Many soil processes are affected by changes in soil water content and movement, for example soil microbial activity and dissolving of SOM (Orchard & Cook 1983; Moyano et al. 2013). Soil microbial and enzymatic activity decreases as soils dry out (Holt 1987; Or et al. 2007). Biogeochemical process rates slow with drying soil (Schimel et al. 2007) and so soil microbial respiration rates decrease with drying soil (Conant et al. 2004; Manzoni & Katul 2014). Also, the dynamics and efficiency of gas transport in the soil is affected by soil moisture and soil structure (Zhang et al. 2018). Soil moisture affects soil respiration directly through physiological processes of roots and microorganisms, and indirectly via diffusion of different substrates and oxygen (O_2) (Yiqi & Zhou 2010). Soil moisture is essential for both plant growth and soil microbial activity, thus affecting carbon inputs and the decomposition of SOM, and hence heterotrophic respiration and carbon outputs (Raich and Schlesinger 1992, Moyano et al. 2013).

Soil fauna has a major role in releasing CO_2 by metabolizing and decomposing SOM (Singh & Gupta 1977). The contribution of soil fauna to soil respiration is usually less than the contribution of soil microbial population (Holt 1987). In arid and semi-arid ecosystems soil fauna, particularly termites has major role in the flow of nutrients and thus in soil respiration. In savannas, soil respiration is counted to be higher during rainy seasons (Hao et al. 1988). When soil moisture is low soil respiration is usually positively related to soil to temperature and they tend to be inversely correlated (Conant et al. 2004). Drought and soil temperatures has increased in East Africa as a result of climate change. Changes in precipitation frequency and intensity have impact on soil respiration (Yiqi & Zhou 2010). Warming climate also typically raises the metabolic rates of both plants and microbes. It has been observed that a 2.43°C change in soil temperature reduces soil moisture by 10 % but increases respiration by 12 % (Wang et al. 2014).

2.3 Termites

Perhaps the most important part of the savanna soil fauna is termites (order Blattodea, formerly Isoptera). They are eusocial insects that inhabit tropical and subtropical regions as far as 40°N and 45°S (Wood et al. 1978) with highest diversity in African rain forests (Jones & Eggleton 2011). African savannas also have the greatest diversity of termite species among the savannas of the world. Globally, there are considered to be about 3500 termite species (Weil & Brady 2017). Termites reach densities of up to 400 termites per m^2 in the soils of dry tropical Africa and they account 40–65 % of the soil fauna biomass (Jones 1990). In African savannas termite biomass has been estimated to be 70–110 kg ha^{-1} (Wood et al. 1978). Termites do not exist in cold regions. Thus, the number of termites globally may increase as the surface temperatures rise because of the climate change.

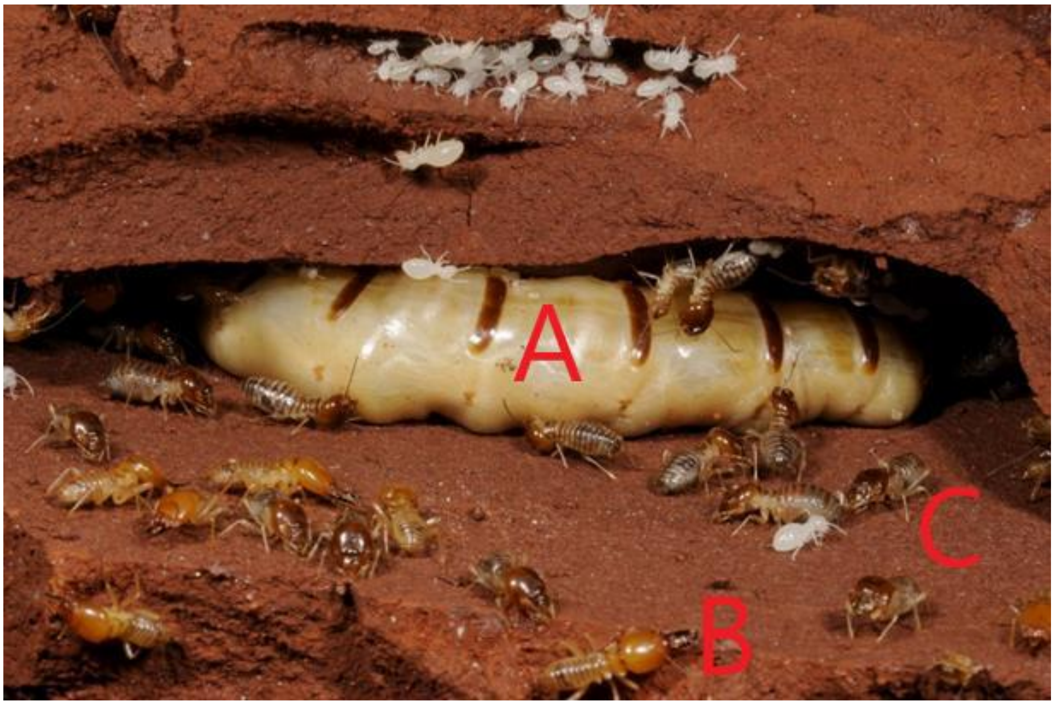

Figure 4: Termites inside Macrotermes nest: A) queen, B) soldier and C) worker (Vesala et al. 2019b, Supplementary Figure S2A).

Termites live in complex social colonies found in about two-thirds of the world's land area. Colony consists queen, king, workers, and soldiers, seen in figure 4 (Eggleton 2010). They build large mounds to provide a home to their colony and to protect their nests (Korb 2010). Mounds can be over 700 years old (Niemelä 2011), up to 12 meters high and extend even deeper into the soil (Weil & Brady 2017). The colony that builds the mound can consist of up to two million termites (Turner 2001). Termites use their saliva and fecal material as cementing agents when building their mounds (Holt & Lepage 2000) which can be seen in figure 5 as rougher part at the top of the mound. When building their mounds, termites transport a considerable amount of soil from lower layers to the surface and thereby mixing the soil. Termites are essentially detritivores; in savannas they are the main user of dead plant material (Holt & Lepage 2000). They feed on almost all the emerging dead plant material at various stages of decomposition and therefore, tropical soil does not accumulate litter or humus in the same way as temperate ecosystem soils (Niemelä 2011). Termites also feed with dung which is important in the recycling of dung of primary consumers, especially herbivores (Freymann et al. 2008).

Figure 5: Termite mound found in Mbula measurement site.

Symbiotic relationship exists between some termites (Macrotermitinae) and fungi (*Termitomyces spp.*). These fungus-growing termites cultivate fungus in their epigeous mounds or in subterranean chambers of mounds. Typical large mounds in Africa are usually build by these fungus-growing termites (Niemelä 2011). Macrotermitinae species feed on a wide selection of dead and living plant material, such as grass, litter, and wood (Eggleton 2000). Worker termites forage in the area surrounding the mound and the fungi is fed with partly digested plant material which has transited through termites (Wood & Thomas 1989). This partly digested plant material is also stored in sponge-like structures, fungus combs, inside the mound. Fungus-growing termites and their fungal symbionts are major litter decomposers in many arid and semi-arid regions in Africa (Jones 1990).

Macrotermitinae species influence the structure and functioning of ecosystems in several ways. They accumulate organic carbon and nutrients into their mounds and degrade them efficiently into CO_2 and thus have a huge impact on carbon cycling (Wood et al. 1978; Lepage et al. 2006). They also strongly modify soil texture and structure when foraging and building their mounds (Holt & Lepage 2000). In this study Macrotermitinae species are represented by *Macrotermes michaelseni* and *Macrotermes subhyalinus.*

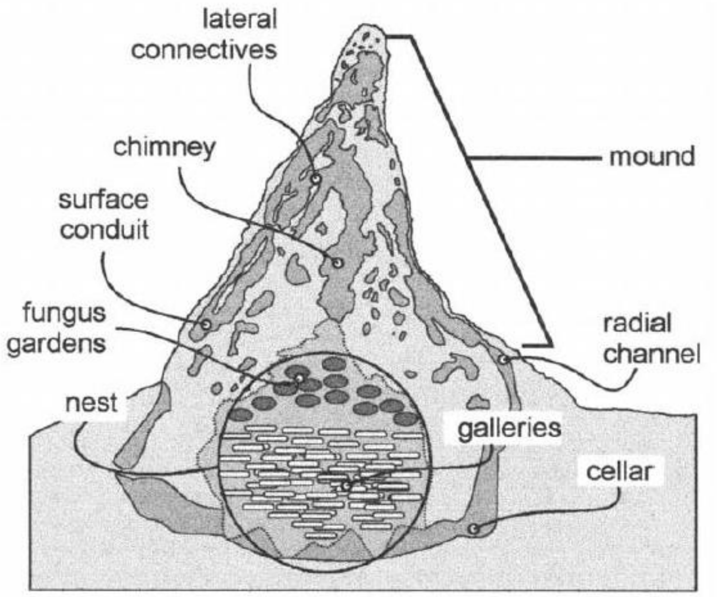

Figure 6: Cross-section of the mound of Macrotermes michaelseni (Turner 2000b).

Termite mounds are built so that the actual nest is subterranean, as seen in the figure 6. The queen, workers, and nursery galleries for reproductives are located in the nest, which is a spherical space about 1.5–2.0 meters in diameter (Turner 2001). Just on top of the nest are chambers housing fungus combs, called fungus gardens. Surrounding the nest is a network of tunnels that extend around and below the nest and merge above the fungus gardens to form a chimney to the center of the mound. The chimney is also a center to the other network of 2–10 cm diameter wide tunnels, that extend throughout the mound, called lateral connectives (Turner 2000a). The lateral connectives merge into a series of vertically oriented surface conduits that underlie roughly 20 % of the mound surface (Turner 2001). The surface conduits are separated from the outside air by a porous, 1–3 cm thick covering. Mound soil properties are primarily determined by those of the parent soil (Pomeroy 1983). Termites bring soil into their mounds from considerable depths, so soils inside the mound often differ considerably from the ambient surface soils (Turner 2006).

2.3.1 Mound ventilation

Termite mounds seek homeostasis. That involves managing fluxes of CO_2, O_2, water, and energy (Turner 2006; Ocko et al. 2017). Subterranean nests and fungal symbionts benefit from stable temperature and moisture conditions. The air inside an active *Macrotermes* nest is much more humid than the atmosphere. Mounds get their water from termite metabolism, trough transport and from deeper soils. In rainy seasons when the walls inside nest are moist, nest temperatures can be regulated by evaporative cooling, where water vapor diffuses out through soil pores (Noirot & Darlington 2000). In dry seasons when this water loss cannot be sustained, the upper parts of the mound are often emptied and left to dry.

Mound structures play a major role in gas exchange, large nests must be effectively ventilated to remove CO_2 and heat generated by the metabolism of termites and their fungal symbiont (Weir 1973; Korb 2003). The simplest way to ventilate nest is to channel the wind into it (Noirot & Darlington 2000). Lateral connectives that are open at both ends work as passages where the air moves through. Air movement depends on wind energy and the internal geometry of the passage system. Changes in wind direction or speed reverse or cease the direction of air flow (Weir 1973). The volume of air passing through the mound is proportional to their size, due to an increase in the number of passages per mound.

Mound air ventilation has a diurnal cycle, daily temperature oscillations drive convective flow, which reverses twice a day (Ocko et al. 2017). Mound structure forms a large thermal gradient between the insulated chimney and exposed passages (King et al. 2015). When passages heat up warmer than the interior of the mound, air flows up in them while pushing down cooler air in the chimney. The opposite happens when the thermal gradient is reversed at night. This creates circulation inside the mound and promotes the flushing of CO_2. Climate and in particular prevailing temperatures influence termite mound architecture, mounds tend to be less complex in cooler habitants (Korb 2003).

The termite species studied are morphologically almost identical but differ in the mounds they build. *Macrotermes subhyalinus* builds larger mounds on average and they have larger queens, a greater biomass of sterile adults, and a greater weight of fungus combs than *Macrotermes michaelseni* (Darlington 1990). Architecturally, the mounds differ in that *Macrotermes subhyalinus* has open ventilation passages while *Macrotermes michaelseni* has closed ones. The ventilation inside mounds of *Macrotermes subhyalinus* is similar to that previously described. Primary ventilation method is wind-induced throughput where at least two openings of passage are required, one raised above the surface and one close to the ground (Korb 2010). When the wind speeds differ in these openings, a negative pressure is induced so that air is drawn into the lower opening from the higher opening. The passages are separated from directly ventilating the nest or fungus gardens by soil layers.

In the mounds of *Macrotermes michaelseni* ventilation is also wind-induced but happens mainly in the porous surface of the mound through diffusion (Korb 2010; Ocko et al. 2017). Ventilation is driven by interaction between architecture of the mound, wind energy and temporal variation of wind speed and direction (Turner 2001). Also, the energy generated by the colony's metabolism affects the ventilation (Korb 2010). Air movement is not circulatory but tidal, air in the mounds of *Macrotermes michaelseni* moves as a convective cell following a diurnally oscillating thermal schedule, since these mounds get large amounts of radiation during daytime (Ocko et al. 2017). Because the mounds are closed, CO_2 concentration inside the nest is higher than in the nests of *Macrotermes subhyalinus* (Noirot & Darlington 2000). Temperatures also tend to be higher inside closed mounds of *Macrotermes michaelseni* (Vesala et al. 2019a). Differences between mounds and their thermoregulation may also explain the respiration rates of the surrounding soil.

2.3.2 Impact on the carbon cycle

Soil fauna including termites have their impact on the soil carbon cycle, in particular, they affect soil respiration (Singh & Gupta 1977; Coleman et al. 1983). Without termites the rate of carbon cycling is regulated by seasonal and diurnal activity of soil microbes and other soil fauna (Jones 1990). The four main reasons for their importance in the soil carbon cycle are their high biomass in many tropical ecosystems, their role in decomposition processes, their impact on soil function, and their role in emitting CO_2 (Sugimoto et al. 2000).

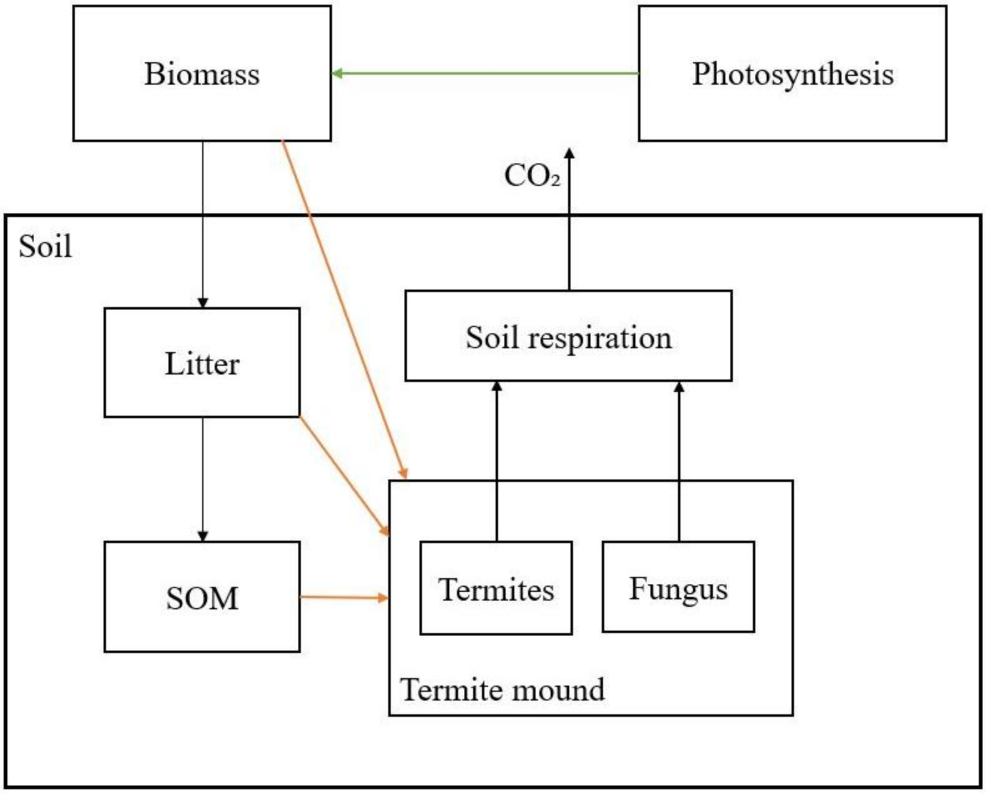

Figure 7: Termite impact on soil carbon dynamics, green line represents photosynthesis and orange lines termite foraging.

In African savanna soils termites was described to be covering 40–65 % of the soil fauna biomass (Jones 1990). In savannas, termites have important role in ecological functioning: being the main decomposers of savannas they process large quantities of dead and living plant material (Holt & Lepage 2000; Brümmer et al. 2009). In Tsavo Ecosystem fungus-growing termites and their symbionts may be responsible for 90 % of wood litter decomposition (Buxton 1981). Decomposition rates are particularly high in soils occupied with Macrotermitinae termites because their foraging activities and fungus cultivation (Jones 1990). As their diet is entirely comprised of autotrophically fixed carbon, termites have significant effect on carbon mineralization and nutrient recycling (Holt & Coventry 1990). By their foraging and mound-building behavior, termites affect soil properties and function. The impact of termites on soil function is described in more detail in the next paragraph.

In savannas high rates of carbon mineralization have been measured in the structures built by macrofauna, such as termite mounds (Lepage 2006). In Australian savanna, termites are responsible for 20 % of all carbon mineralization in soils (Holt 1987). In African soils, the rates are presumably similar. Termites contribute soil respiration with CO_2 emissions from respiration by live tissues (termites themselves and fungal tissue) and their nest metabolism that generates CO_2 as waste product (Noirot & Darlington 2000; Konaté et al. 2003). Large termite nests may have total CO_2 outflow of

800–1500 l d^{-1} (Darlington et al. 1997). CO_2 emissions from single termite from *Macrotermes spp.* is estimated to be 0.501 mg CO_2 g $termite^{-1}$ h^{-1} (Sanderson 1996).

Environmental factors, such as temperature, moisture, or food quantity and quality can affect to the rates of termite metabolism and respiration (Jamali et al. 2011). Estimates of the total respiration of termite community can be calculated with population data. Mound population and mound volume are usually closely correlated (Lepage & Darlington 2000). In colonies of *Macrotermes michaelseni* and *Macrotermes subhyalinus*, the fresh weight of termite queen is positively correlated with the parameters of mound size, population and volume. In the mounds of Macrotermes subhyalinus the weight of termite queen positively correlated also with the number of open-air passages (Darlington 1990). Seasonal variation in CO_2 emissions can be caused by a change in the number of termites inside mound (Jamali et al. 2011). Mound CO_2 emissions can be 3.5 times higher in the wet season because the termite biomass inside the mound can be even 10 times greater. Seasonal variation in termite activity such as foraging outside the mounds can also affect the amount of CO_2 emissions. Nevertheless, although Brümmer et al. (2009) estimated the contribution of termites to the be only 0.4 % of total savanna soil CO_2 emissions, their effect on carbon cycle and the area around their mounds is significant.

2.3.3 Impact on the surrounding area

Soil physical properties like porosity, bulk density and infiltration are primarily determined by soil type, but are modified by the activities of soil organisms, such as termites (Dangerfield et al. 1998). Termite activity causes physical disturbance of soil profiles and changes the soil texture, the distribution of organic matter, and the soil nutrient content (Wood 1988; Jones 1990; Pringle & Tarnita 2017). Termites modify surrounding soils when building their mounds and when they forage outside their mounds.

When building their mounds, fungus-growing termites have major effects on soil chemical and physical properties (Dangerfield et al. 1998). Building of the mound and especially subterranean nest and fungus galleries have a strong influence on the soil profile development (Holt & Lepage 2000). Mound soils usually have higher bulk density and reduced porosity because termites repack and cement together soil particles when building their mounds. However, subterranean nest and fungus galleries increase soil porosity and improve soil water transmission properties. Soil chemical properties change when termites mix soil mineral particles with organic compounds, with the addition of water from their salivary secretion when building their mounds. While building their mound, the termites also bring clay and from sub-soils. Erosion of the mound provides nutrients to the surface soil. In savannas predators and sometimes the prey use high termite mounds as observation stations and may also defecate on them, which also brings nutrients to the surface soil. With the higher clay and nutrient content, and soil water availability soils around termite mound may have better conditions for plant growth (Joseph et al. 2014). Termites may sometimes also have a negative effect on plant growth around their mounds by foraging roots or above-ground plant material.

Fungus-growing termite densities in savanna soils can be even 400 termites per m^2 (Jones 1990). Termites have a foraging zone that may extend 35–50 meters from their mound, with the nearest neighbor mound being 50–80 meters away (figure 8). Large termite mounds are often farther apart than small ones (Pringle & Tarnita 2017). Closer neighbors compete more intensively, and mound densities tend to increase with food resource availability. Therefore, foraging from different colonies can cover most of the available land area in savannas (Dangerfield et al. 1998). Foraging tunnels build by *Macrotermes michaelseni* can cover even 366 ml m^2 in soil (Darlington 1982).

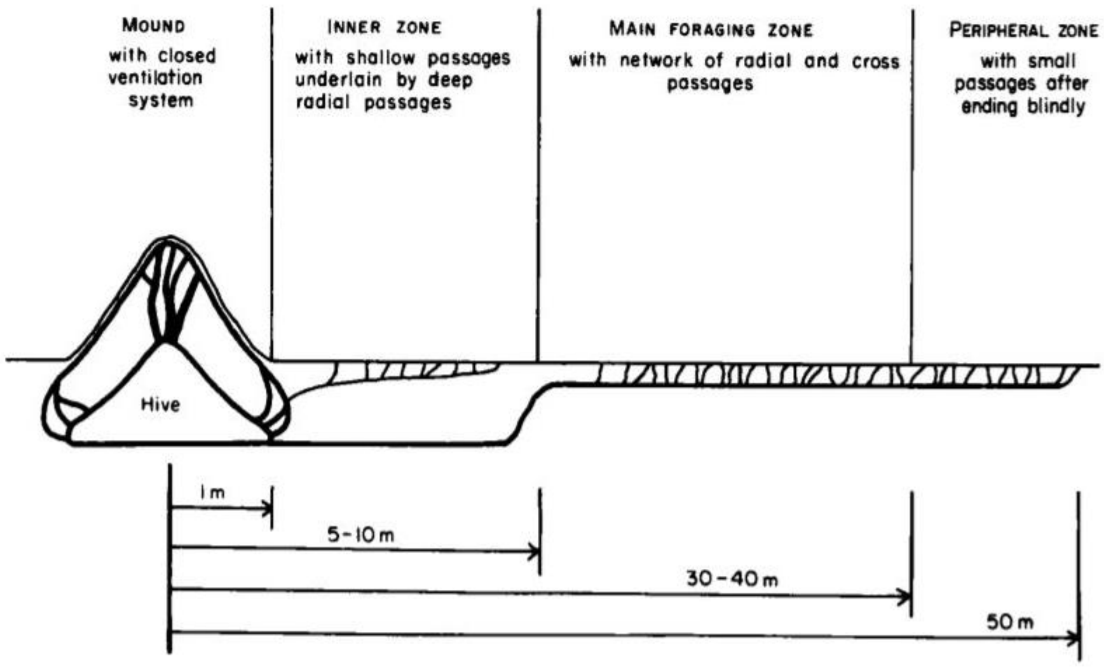

Figure 8: Mound and subterranean passage system of Macrotermes michaelseni (Darlington 1982).

Most termites built subterranean foraging tunnels (Holt & Lepage 2000). In the closed mounds of *Macrotermes michaelseni* the foraging tunnels leave from the edges of their nest and radiate out at 50‒80 cm below the soil surface before emerging to the surface about 5‒10 meters from the mound (Darlington 1982). This area around the mound is called the inner zone (figure 8). The main foraging zone is from about 10‒35 meters from the mound. Only during severe drought, when there is not much food in the main foraging zone, termites tend to forage in the inner zone (Lepage 1976). Low foraging intensity in the inner zone may affect to the differences in vegetation and soil observed around the mounds (Arshad 1982). Foraging tunnels around the mounds can radiate for even 50 meters or more into surrounding soils (Turner 2006). These tunnels are not permanent structures, when the rain wets the soil, foraging tunnels and the foraging access passages into the mound collapse and thus prevent the flooding of the mound (Darlington 1982). New access passages and foraging tunnels are built as needed. Termites also build protective soil sheetings as they move on the soil surface in order to protect themselves from predators and from drying out (Holt & Lepage 2000). These soil sheeting were often visible at measurement sites in this study.

Building of these foraging tunnels affects soil hydrology and movement of water through termite nests (Turner 2006). Building also cause substantial upward transport of soil which increases the volume of soil macropores and thus infiltration and accumulation of rainfall around the mound. For example, soil moisture availability is usually highest 1–10 meters from the mound (Arshad 1982). Soil fauna also influences on soil macroporosity. High macroporosity means that the resistance of the soil to the diffusion of gases by concentration gradients is low. For example, soil water content at holding capacity is around four times higher on termite mounds than elsewhere in the savannas (Abbadie et al. 2006).

3 RESEARCH AREA

Both study sites are semi-arid savannas in Tsavo ecosystem located next to Taita Hills in Taita-Taveta County in southeast Kenya. Taita Hills represent the northern part of the Eastern Arc Mountains extending from southern Tanzania to southeast Kenya (Lovett and Wasser 1993). Geologically, the area is underlain by up to 2.5 billion years old Precambrian basement rocks (WWF 2001). Buxton described in his study (1981) the soil type in the Tsavo ecosystem to be mostly deep, acidic red sandy clay with low fertility (rhodic ferralsol).

Taita Research Station of University of Helsinki is located near study sites and extensive multidisciplinary research has been made in the surrounding area at least since 1989. For example, the same termite mounds have been studied extensively: geological (Leppäniemi 2019) and biological analysis (Vesala et al. 2017; Vesala et al. 2019b), mound thermal conditions (Vesala et al. 2019a), CO_2 and CH_4 emissions from the mound (unpublished) and from the termites themselves are studied. Possibility to link different kinds of research about the same subjects allows more comprehensive understanding of them and makes the dataset more valuable for further research.

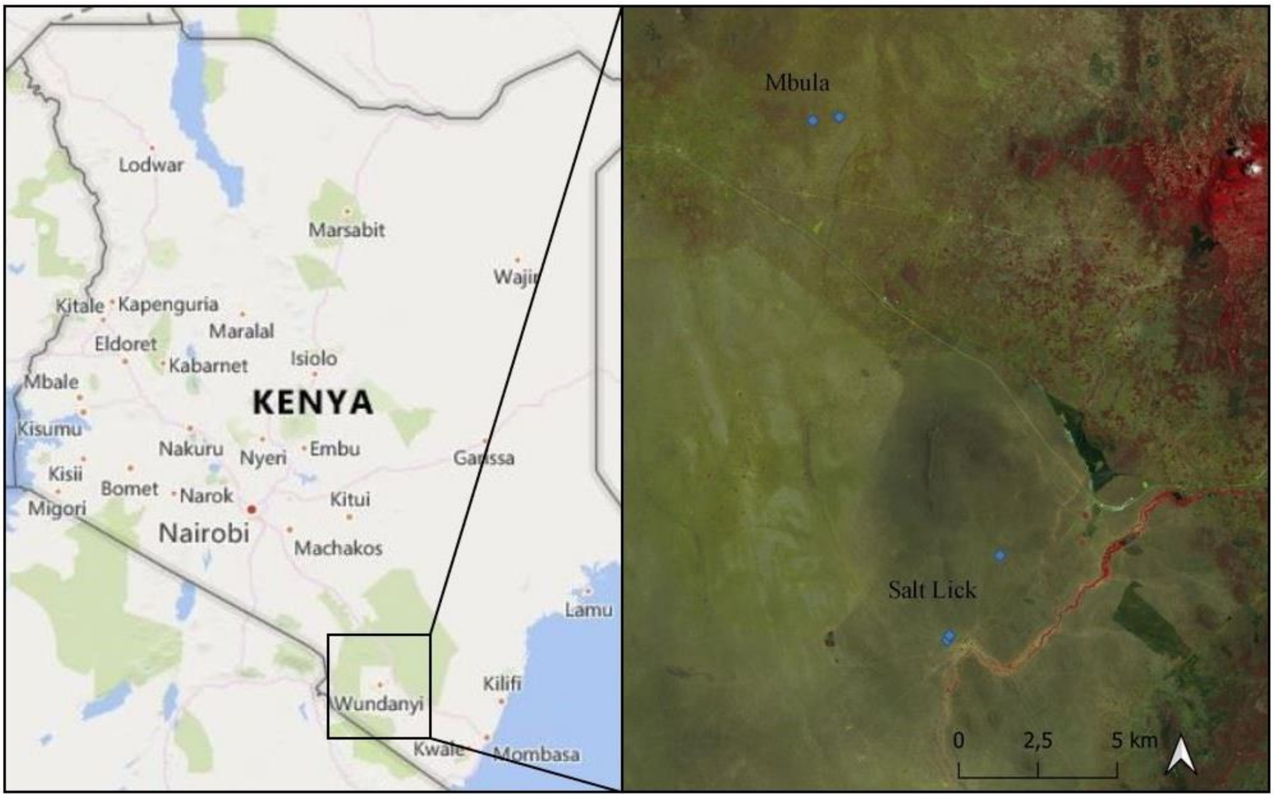

Figure 9: Map of Kenya and close-up from the area around study sites Salt Lick and Mbula in south-eastern Kenya. About 80 % of the total land area in Kenya is classified as savanna and grassland ecosystems.

The mean annual temperature of the area is *ca.* 25°C and the mean annual precipitation *ca.* 600 mm. Most of the rainfall occurs in two rainy seasons due to the movement of the ITCZ over the equator in March–May (long rains) and November–December (short rains), as seen in figure 10. Rains are typically erratic, so droughts are unfortunately common in the area (Vesala et al. 2017). Trade winds blow from the northeast in January and from the southeast in April.

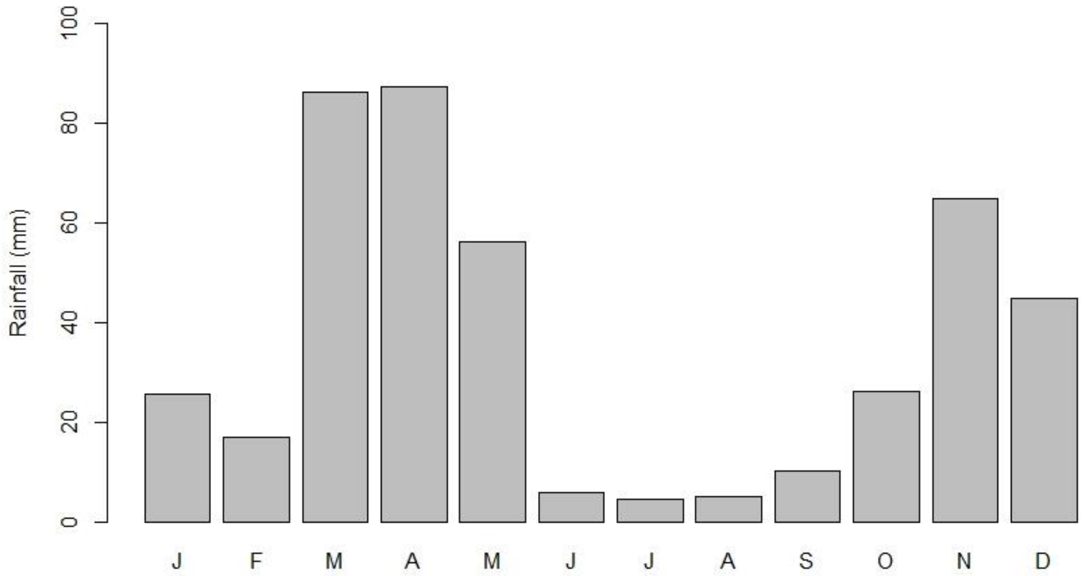

Figure 10: Monthly average rainfall from Maktau weather station (September 2013-August 2019).

Measurements were made in three campaigns: 6.-18.11.2016, 16.-24.04.2017, and 10.-12.12.2017. Even though all measurement months took place in the supposed rainy season, weather conditions varied a lot between them. Vegetation greenness, soil moisture and amount of rainfall varied the most between measurement periods, though simultaneously air and soil temperatures stayed similar through all three measurement periods.

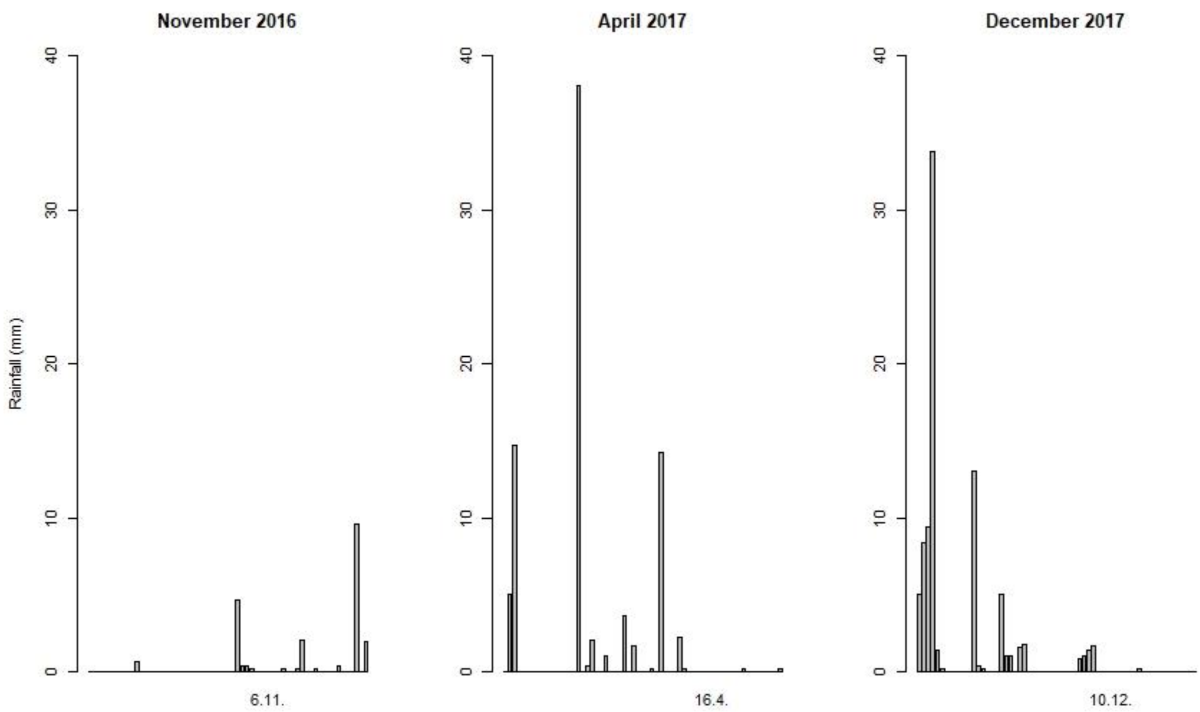

Figure 11: Daily rainfall during measurement periods and from month before them. Dates represent the starting day of each measurements.

Initially, five termite mounds from Salt Lick and four termite mounds from Mbula was measured, but due either drought, intentional or accidental damaging, or other disturbances three of the mounds were abandoned between second and third measurement period. The final number of mounds used in this study ended up being three from both sites. In the area, termite mound densities are mostly high, and mounds are clearly visible from aerial photographs. Most of the termites found in the study area represent these two fungus-growing termite species *Macrotermes michaelseni* and *Macrotermes subhyalinus.* Names of sites and part of the environmental parameters are according to the study by Vesala et al. (2017) from the same measurement sites.

Table 1. Termite mounds used in this study.

Name	Height (cm)	Width (cm)	Volume (m^3)	Mound type	Termite species
S1	70	220	0.89	closed	*M. michaelseni*
S2	35	130	0.15	closed	*M. michaelseni*
S5	40	200	0.89	open	*M. subhyalinus*
MR1	50	300	1.18	closed	*M. michaelseni*
MR2	15	130	0.07	open	*M. subhyalinus*
MR4	45	180	0.38	open	*M. subhyalinus*

3.1 Mbula measurement site

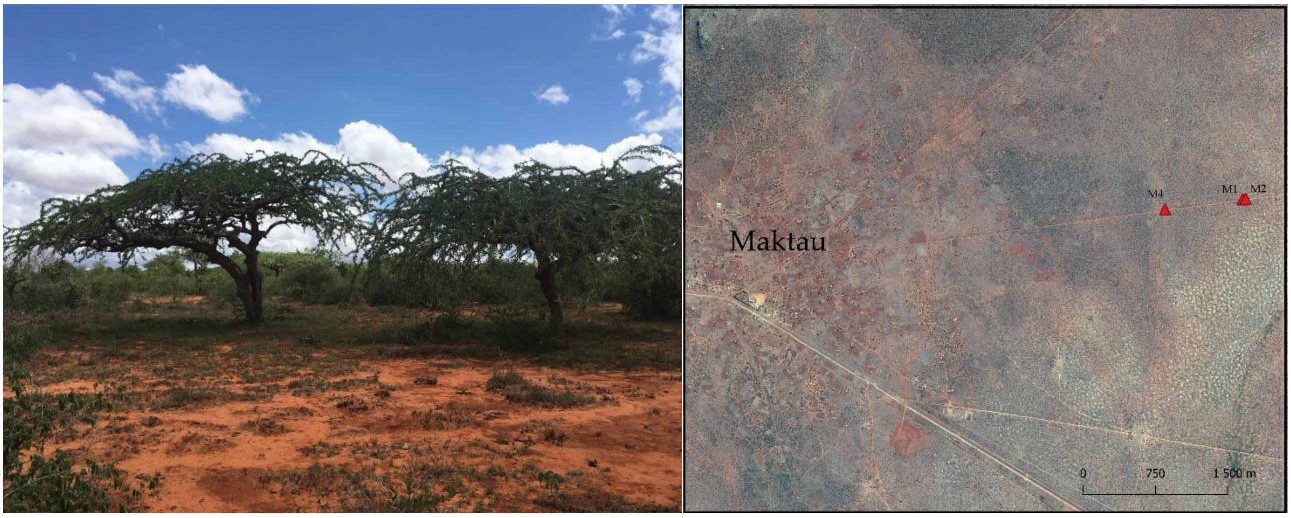

Figure 12: On the left picture from the Mbula study site in April 2017, on the right map of the study area and mounds MR1, MR2 and MR4. Maktau weather station is located few kilometers south from Maktau town.

The study site of Mbula is located along Mwanda Road leaving from nearby Maktau town. Mounds are located next to an unpaved road in the middle of partly thick bushes. Except for occasional cars, motorcycles and carts the road section is quite quiet. However, many large herds of cattle and their owners are moving around in the area. It came to be noticed that local people deliberately destroyed the mounds that were measured, apparently in the fear of somehow losing their lands. Mounds were also abandoned possibly due to drought. Out of the four original mounds only three survived throughout the measurement period.

Vesala et al. (2017) described the area to be dense shrubland with scattered small trees, including *Acacia* and *Grewia spp.* as seen in figure 12. The most common grasses around the measured mounds in both measurement sites were *Cynodon dactylon* and *Chlorix roxburghiana*. Woody vegetation covers *ca.* 60 % of the study area and despite the amount of vegetation, the area is really dry. Elevation in the area is 1050 meters above sea-level, density of active termite colonies is 1.5 ha and soil is typical red ferralsol.

3.2 Salt Lick measurement site

Figure 13: On the left view from the mound S2 in Salt Lick after drought in November 2016. Vegetation in the area was much greener on the other measurement periods. On the right map of the study area and mounds S1, S2 and S5.

The study site of Salt Lick is located in Taita Hills Wildlife Sanctuary, near Sarova Salt Lick Game Lodge. All the mounds are located in the middle of savanna where only animals of the park pass. Large numbers of elephants have inflicted widespread destruction on the original woody cover of the park, leading to a complete change in land type. Conservancy is fenced and difference between the park and surrounding area is visible in aerial photography. Due to overgrazing and other damage by elephants together with droughts, termites tend to abandon their nests unfortunately often in the area. Out of the five original mounds only three survived throughout the measurement period.

Vesala et al. (2017) described the area to be open grassland with scattered and predominately damaged trees, mostly *Acacia spp.* as seen in figure 13. Woody vegetation covers only 1 % of the study area. Elevation in the area is 890 meters above sea-level and density of active termite colonies is 0.2 ha, which is considerably smaller than in Mbula site. Most of the mounds in the area are abandoned. Soil is mostly red ferralsol, but white calcisol is also present in the soil and therefore some of the mounds in the area, but not in any of the mounds used in this study.

4 MATERIAL AND METHODS

4.1 Chamber method

In this study soil respiration measurements were made using the closed static chamber method (Livingston & Hutchinson 1995; Pumpanen et. al 2004). Under these circumstances, where distances were long and measurement conditions were challenging, this method was the easiest to implement. Portability and simplicity of studying spatial variation were the major advantages of this method (Matsuura et al. 2011).

In the closed static chamber method part of the soil surface is covered with an air-tight chamber. CO_2 released from the soil accumulates inside the chamber and its amount begins to rise. The rate of CO_2 increase is proportional to the soil respiration (Yiqi & Zhou 2010). To determine soil respiration rate CO_2-detecting sensor is used to measure the increase in chamber CO_2 concentration over time. When the start and end value are known the increment in the amount of CO_2 concentration inside the chamber can be used to estimate the rate of soil respiration (F) with the following equation (Field et al. 2000):

$$F = \frac{(c_f - c_i)V}{\Delta t A} \tag{2}$$

where c_i is the initial and c_f is the final CO_2 concentration inside the chamber, V is the total system volume, Δt is the time between CO_2 measurement points and A is the total soil surface area covered by the chamber (Yiqi & Zhou 2010). All the measured values in this study has been obtained using this equation.

The chamber (figure 14) used in this study was designed by Jukka Pumpanen at the University of Helsinki (Pumpanen et al. 2004). This closed static chamber (NSNF-3) is made of polycarbonate, its diameter is 200 mm and height 300 mm. It also had a small fan attached to its ceiling to ensure proper vertical air mixing inside the chamber. Two sensors were connected to the chamber: infrared based CO_2-detecting sensor (IRGA) (GMP343; Vaisala, Vantaa, Finland) and temperature/humidity sensor (HM70; Vaisala, Vantaa, Finland). Sensors were connected to data-logging device (MI70; Vaisala, Vantaa, Finland) which allowed real-time monitoring of the measurements. The IRGA has a built-in internal compensation designed to minimize the effects of different environmental parameters to measurements. For example, atmospheric pressure values had to be manually applied before measurements.

Figure 14: Measuring instruments: NSNF-3 chamber on top of the metal collar, data-logger and the two sensors on top of the chamber. Another metal collar is visible in the background. The battery is for the small fan located inside the chamber.

4.2 Respiration data

Three replicates of soil respiration measurements were done in one measurement point and average values from them was used in this study. The measurement time was selected to be two minutes with 30 second logging interval, whereby each measurement received five CO_2 concentration values. In this way, the battery was saved, and it was secured that all the data fitted in the memory of data-logging device. If the battery from the device had run out, all the collected material would have been lost. Measurements were done 1 and 2 meters from the mound from three directions (figure 15), that varied slightly depending on the conditions at the measurement site. Site-specific directions were chosen so that there was no need to measure in the middle of thorny shrubs or destroy the surrounding vegetation because of the measurements. A reference measurement was also taken 10 meters from mounds in December 2017, because it was assumed that the foraging zone of termites would start from there and it would reflect the normal soil respiration of savannas.

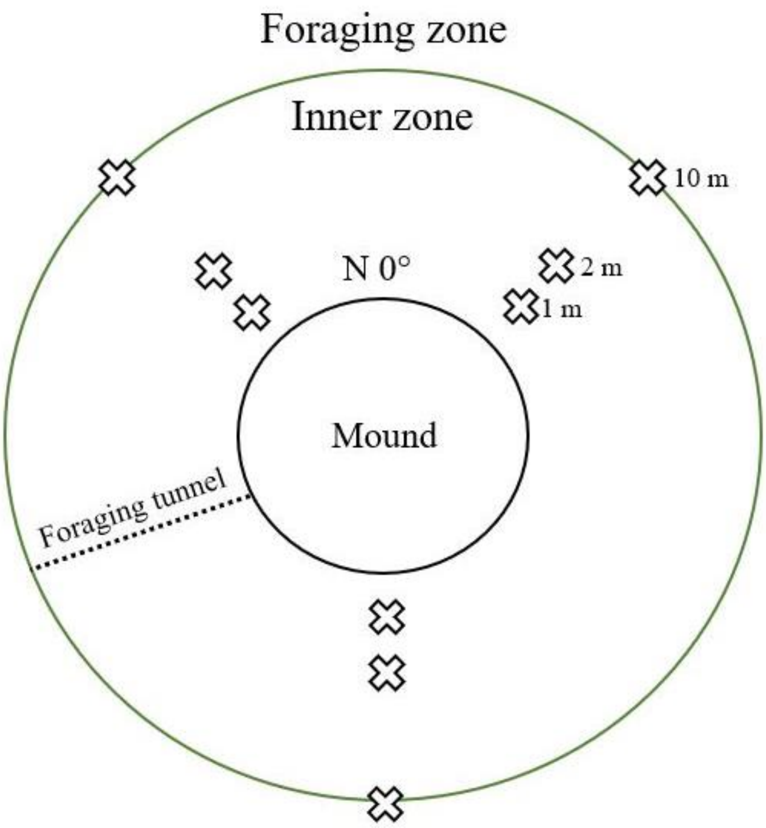

Figure 15: Measurement set-up, crosses represent measurement points 1,2 and 10 meters from the mound in directions of 60°, 180° and 300°.

As seen in figure 14, soil respiration was measured from vegetation-free spots and all of the possible dry litter was removed. Metal collars were initially attempted to be inserted into the soil but due to the drought they were left on top of the soil and were made as airtight as possible by surrounding them with excavated soil. Bungee cords attached to the collar were also used to ensure airtightness inside the chamber during measurements. Collars were placed to the soil about 15 minutes before measurements. The chamber was protected from solar radiation first with a thick plastic cover and an umbrella, but later it was properly wrapped in foil. In this way, the chamber was essentially prevented from overheating under savanna conditions since the air inside the chamber should not heat significantly because it would distort the results (Livingston & Hutchinson 1995). This also prevented possible photosynthesis although there was only a little vegetation at the measurement sites.

The obtained measurement results were extracted using software provided by Vaisala which saved the files in their own format, *.M70. As a pre-treatment, all clearly incorrect measurements were discarded from the data. Fortunately, there were only a few of them. Some of the measurements showed that breathing air, for example, had entered the chamber or that the data was otherwise problematic or even ruined. If the data showed uncontrollably large increases in carbon content or strange jumps and fluctuations when visualized it was rejected. For this reason, it was good to be able to view the measurements already in the field and renew all potentially failed ones. Measurement data and other necessary information were then inserted to Microsoft Excel spreadsheet, where soil respiration was calculated using the previous equation (eq. 2). The results obtained were in the form of µmol CO_2 m^{-2} s^{-2} but were converted to commonly used form mg CO_2 m^{-2} h^{-1}. Finally, the data was analyzed and processed into graphs using R 3.5.1 (R Core Team).

4.3 Meteorological measurements

Other measurements included soil moisture and soil temperature measurements. Prevailing atmospheric pressure varied between measurement seasons, so pressure values were also measured using barometer and applied manually before each measurements. Soil temperature was measured from several points around the measurement area by using simple laboratory thermometer. Average temperatures ware used since there were only little variation in soil temperatures inside the area. Soil moisture was measured using a device (HydroSense II; Campbell Scientific, Utah, United States) for measuring soil volumetric water content (% VWC). There were also very small variance in soil moisture so similarly averages of soil moisture measurements are used. Smallest measured soil moisture values were just 1 % with the accuracy of ±3 % (Campbell Scientific 2014). Almost nothing in the measurement area creates variance because the soil was sandy, rainfall low and there was little surface vegetation that would bind moisture to the soil. Measurement depth on both soil moisture and temperature was 10 cm due to soil drought. Setting the measuring devices deeper into soil was almost impossible.

Meteorological data for the area was obtained from the Maktau weather station of the Taita Research Station located about 10 km from the measurement sites. Meteorological data obtained included the wind direction and amount of rainfall from September 2016 to August 2018. Information about mound parameters, basal width and height for counting the estimated above-ground mound volume, type of the mound and inhabiting termite species were obtained from Risto Vesala, since his research (Vesala et al. 2017; Vesala et al. 2019a; Vesala et al. 2019b) focused on these same mounds.

After the last measurements in December 2017 surface soil was removed from all the measuring points and organic material such as roots or possible subterranean passages was observed visually. Neither was clearly visible and no life inside the soil was observed. Additionally, after the last measurements the mounds were dismantled by German scientists as they attempt to research CO_2 emissions from individual termites and fungus. This will give more realistic understanding about the actual size of the mound and total CO_2 emissions of termite colony. Hopefully more information about these mounds will be available in the future so that the research, results and understanding can be deepened, and the mounds were not destroyed in vain.

5 RESULTS

The results sought to answer the research questions posed. Although the measurements went otherwise well, it was found that termite colonies in mounds S1 and MR2 had probably died and mounds were abandoned at some point between April and December 2017. Also, it was found that the activity on mound S2 was very low in all measurement periods, i.e. the termite colony was potentially weak. These factors affected the size of the final dataset, but also allowed a comparison with termite emptied mounds in both measurement sites.

5.1 Respiration around the mound

It has been proven that termites are active outside their mound because, for example, foraging and forage passage building. By calculating the average soil respiration of the measurement points around the mound, the activity of termites around the mound can be observed. The activity of termites was studied as the variation within and between the mounds, the relationship between type of mound and soil respiration, and the relationship between mound size and soil respiration.

It can be assumed that at a distance of 2 meters from the mound, increase in soil respiration would indicate increased termite activity. When looking at variations in soil respiration around mounds, the activity of termites within and between mounds, and the average of all mounds can be compared. Figures 16 and 17 represent soil respiration averages 2 meters from the mound. Soil respiration averages are calculated from three directions, except for mounds MR2 and MR4 from two directions, due to challenging measurement conditions. The highest rates of soil respiration were measured from Salt Lick in December 2017 (*ca.* 700 mg CO_2 m^{-2} h^{-1}) and the lowest rates from Mbula in November 2016 (*ca.* 50 mg CO_2 m^{-2} h^{-1}). These two measurement periods were chosen to visualize the results due to their major differences in soil moisture.

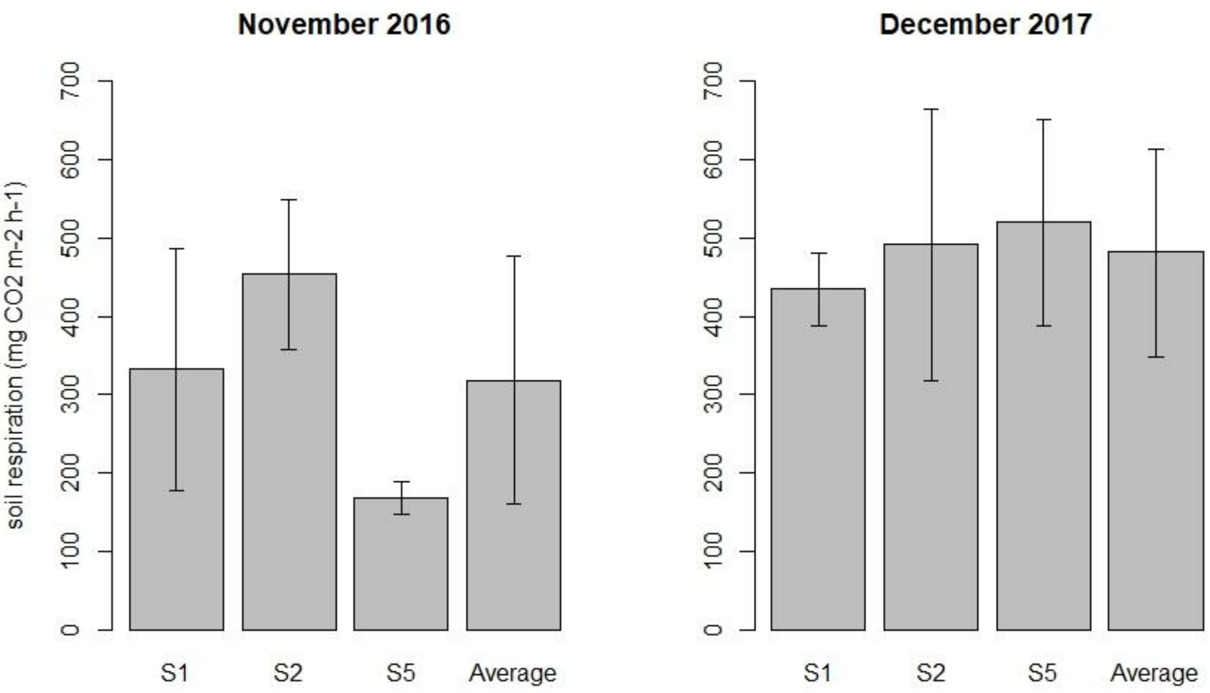

Figure 16: Variation of soil respiration around mounds S1, S2 and S5 in Salt Lick measured at the distance of 2 meters.

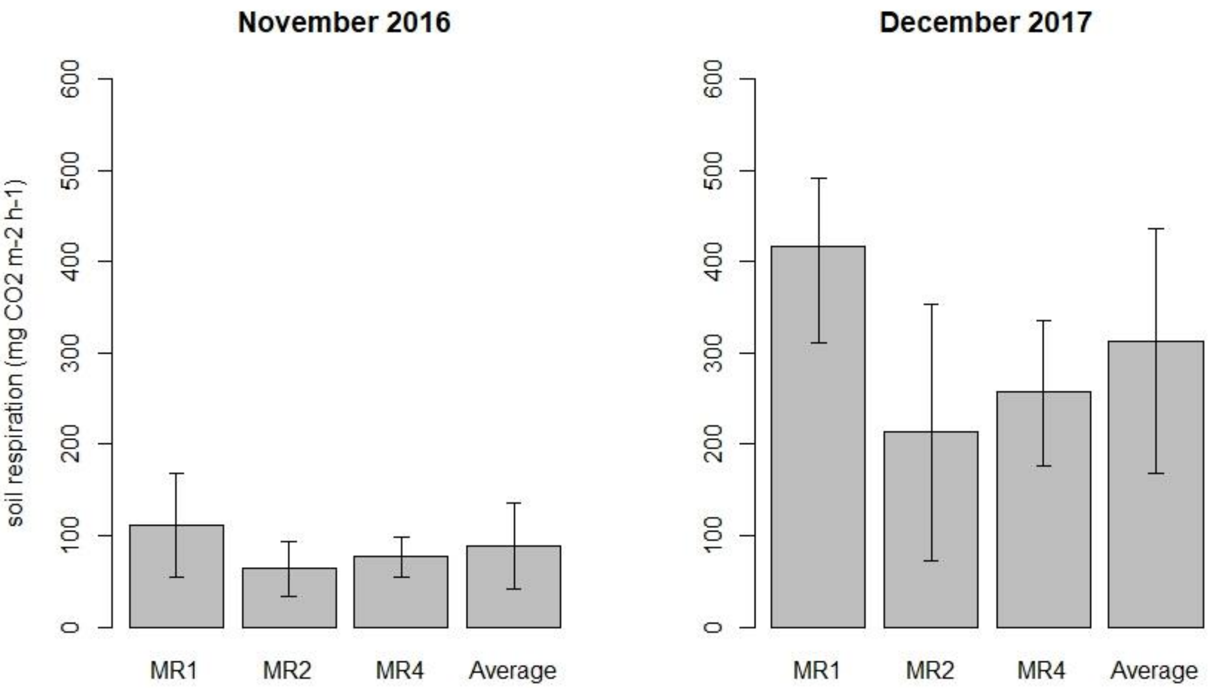

Figure 17: Variation of soil respiration around mounds MR1, MR2 and MR4 in Mbula measured at the distance of 2 meters.

In Salt Lick (figure 16) between the dry and rainy season, soil moisture tripled, and average soil respiration rates increased 75 %. Soil respiration rates increased between measurement periods especially around mound S5. Mound S1 was abandoned between measurement periods, so soil respiration rates around it were the lowest, and its standard deviation was the smallest in December 2017. Because the activity in mound S2 was weak throughout the measurement periods, due to the probable weak colony, respiration rates around it did not increase much between the measurement periods. Despite the weakness of the termite colony, soil respiration rates were high around the mound, so it can be assumed that in this case the activity of the termites did not affect soil respiration. The variation within the mounds was highest in the mound S1 in November 2016 and in the mounds S2 and S5 in December 2017. The variation was very small in the mound S5 in November 2016, so the change between measurement periods was considerable.

In Mbula (figure 17) soil moisture increased 11-fold and soil respiration rates increased 243 % between seasons. The change between measurement periods is noticeable and is clearly seen in the figure 17. Soil respiration rates increased the most around the mound MR1, which was the largest of the mounds, but also considerably around the mound MR4. Mound MR2 was also abandoned between measurement periods, so in December soil respiration rates were lowest around it. Despite this, the standard deviation between soil respiration rates was really large. The variation within mounds in November 2016 were highest in MR1, however, it was not very large in any of the mounds because the soil was so dry, and the rates of soil respiration were low. It was noteworthy, that the ratio of soil respiration rates between the mounds remained the same between measurement periods, and the largest rates were measured around the largest mound. Averages of soil respiration around all mounds varied much in both measurement periods from both measurement sites. This indicates that there was a great deal of variation and difference between the mounds.

The relationship between of mound type and soil respiration can also be observed from the same results. The relationship was studied by counting the estimated volume of above-ground portion of the mound, from the basal width and height data observed and compared it to the seasonal averages of soil respiration around the mound. Mound population and mound volume are known to be closely correlated so it was assumed that larger mounds would have higher termite activity and thus higher soil respiration rates around them. Usually *Macrotermes subhyalinus* tend to have larger mounds than *Macrotermes michaelseni,* but in this study the mounds of *Macrotermes michaelseni* were slightly larger. The biggest increase in soil respiration rates between measurement periods were around mounds MR4 and S5, which both belong to *Macrotermes subhyalinus,* and MR1, which belonged to *Macrotermes michaelseni* and was the largest mound measured. Comparison of the effect of activity on soil respiration between these two termite species is not very relevant due to limited data. With only four mounds alive in December 2017 only a few observations can be made. In November 2016 when all the mounds were alive, soil respiration rates around the mounds of *Macrotermes michaelseni* were higher. In December 2017, there were no significant differences in soil respiration rates around the mounds of different termite species. With this material, no significant correlations were found between the mound size and soil respiration rate. Also, although both the mounds of *Macrotermes michaelseni* and soil respiration rates around them were higher in November 2016, no significant correlations were found for mound volumes and soil respiration rates.

5.2 Effect of wind direction on respiration

The prevailing wind direction that changes with the movement of the ITCZ can affect the amount of soil respiration around the mound. The wind blows through the ventilation of the mound and brings metabolic gases formed by the termites and the fungus with it. In the mounds of *Macrotermes subhyalinus*, ventilation occurs from the passages located near ground when wind generates negative pressure inside the mound. Ventilation in the mounds of *Macrotermes michaelseni* occurs mainly in the porous surface of the mound through diffusion. The assumption is that CO_2 will also potentially exit through the subterranean tunnel network of the mound. Thus, when the wind hits the mound from a certain direction, soil respiration on the opposite side will get higher rates than on the windward side. In figures 18 and 19 soil respiration is visualized from two different distances in order to compare their differences. The measurements are from Salt Lick only due to the dense vegetation in Mbula measurement site. Dense vegetation would have possibly prevented the wind, so accurate measurement results might not have been obtained.

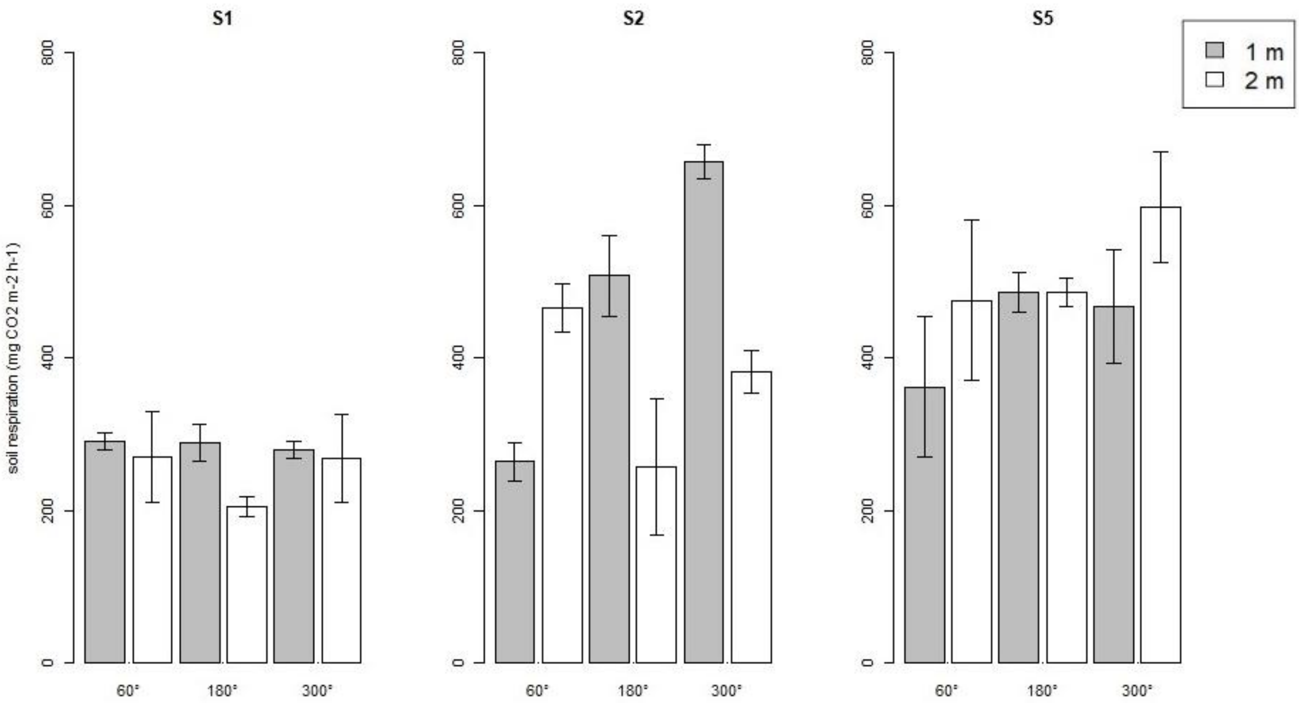

Figure 18: Soil respiration around mounds S1, S2 and S5 in April 2017, prevailing wind from southeast (150°).

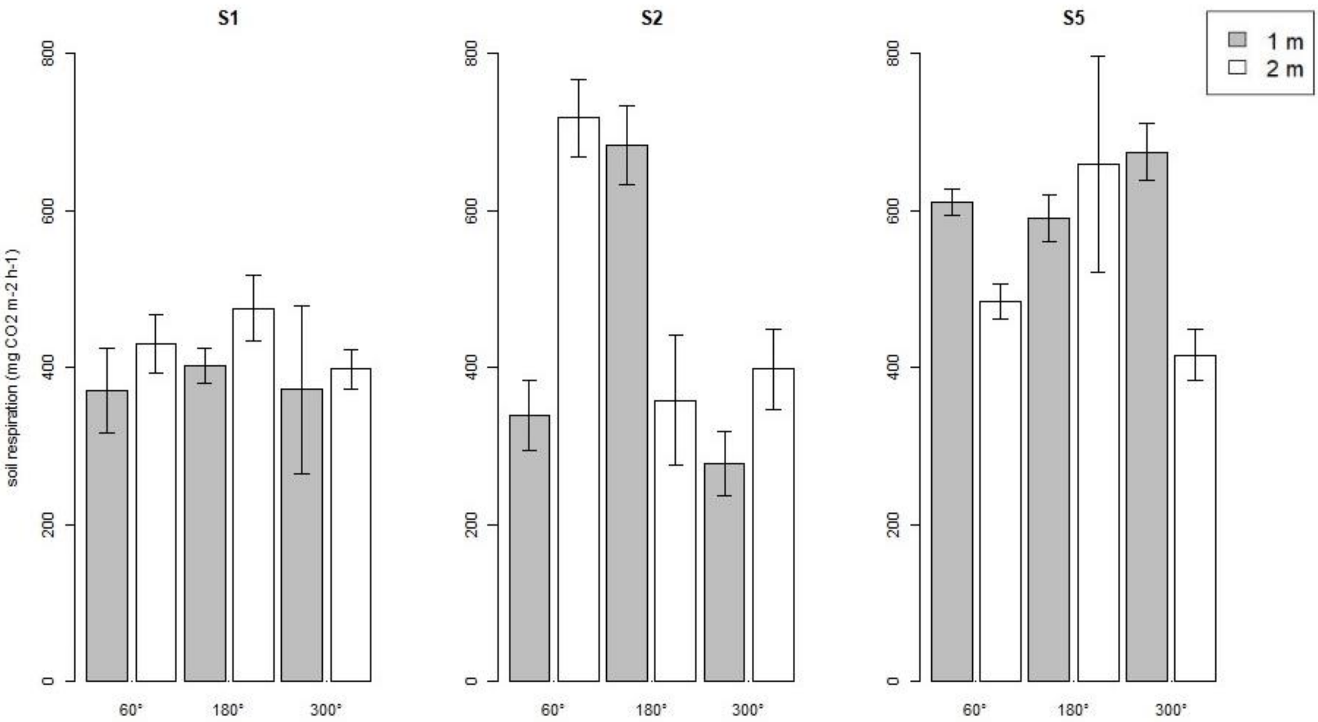

Figure 19: Soil respiration around mounds S1, S2 and S5 in December 2017, prevailing wind from northeast (40°).

In April 2017 (figure 18) the prevailing wind direction was from the southeast (150°) so soil respiration should have gotten the highest rates at 300° from the mounds. The hypothesis was true at a distance of 1 meter for the mound S2 but was not true for the mounds S1 and S5. From the distance of 2 meters, the hypothesis was true for mounds S1 and S5. In all mounds, soil respiration rates at a distance of 2 meters was lowest near the windward direction, at 180°. Looking at the April 2017 values, it can be stated that the hypothesis was true at a distance of 2 meters from the mound.

In December 2017 (figure 19) the prevailing wind direction was from the northeast (40°), so soil respiration should have gotten highest rates at 180° from the mounds. At the distance of 1 meter from the mound S2, soil respiration rates were in line with the hypothesis. Around the mound S5 soil respiration rates were equal in each direction, so they were presumably not affected by the wind. At the distance of 2 meters from the mound S5, there were significantly higher soil respiration rates from the direction of 180°. The mound S2 had the exact opposite situation and soil respiration was highest in the windward direction. Unlike in April 2017, these values can hardly be seen to fulfill the hypothesis, partly due to the small number of observations. In December 2017, the mound S1 had been abandoned, so soil respiration rates and their variation were negligible. Despite the uninhabitation, soil respiration on mound S1 were on average slightly higher in the direction of 180° at both 1- and 2-meter distance. This is irrelevant to the hypothesis since the rates were not related to termites and the differences between them were minor.

From the results of the surviving mounds it can be concluded that for the open mound S5 the hypothesis was true at the distance of 2 meters, but not in the distance of 1 meter. In the case of closed mound S2, the opposite happened, and the hypothesis was true 1 meter from the mound but not in the distance of 2 meters. The standard deviation between measurements was small because the measurements were made at the same points. The variation was greatest in December 2017 at two meters from mound S5 at direction of 180°. All of the mounds were measured on different days, so wind speed and gust certainly varied in measurement times. Mound and ventilation type can also have an effect: air passing through closed and open mounds may behave differently when leaving the mound, thus affecting the amount of exiting CO_2 and soil respiration rates. In addition, the size of the mound may affect as the volume of air passing through the mound is proportional to the size of the mound. Because mound S1 was likely dead in December 2017, rates of soil respiration around it was lower and the mean variation was also smaller than in the other mounds.

5.3 Meteorological parameters

Meteorological parameters soil moisture, soil temperature, and seasonal rainfall was compared to soil respiration rates. Rainfall obtained at Maktau weather station varied a lot between measurement periods. The first measurement period was extremely dry: before first measurements rainfall was only 0.6 mm in October 2016 and 20.2 mm in November 2016, which was significantly lower than the regional averages (figure 10). Before second measurement rainfall in March 2017 was 66.8 mm and 17.2 mm in April 2017, so these amounts were also below average. Before last measurements rainfall was 82.2 mm in November 2017 and 5.2 in December 2017. These amounts, in turn, exceeded regional averages. Thus, the rainfall was significantly higher in the second and third measurement periods and in the months preceding them (figure 11). In the long run, higher rainfall increased soil moisture, which can be seen in figure 21.

Previous studies show that soil respiration rates are mostly affected by soil moisture and soil temperature, so their effect was studied in more detail. Soil moisture values varied widely between measurement periods (figure 21). Soil temperatures were slightly higher in Mbula, while soil moisture was significantly higher in Salt Lick in all measurement periods. A strong positive correlation ($R^2 = 0.81$) was found between changes in soil moisture and soil respiration, so it was the main explanatory variable in the changes of soil respiration rates. The variation in soil temperatures was small and temperatures were relatively high throughout the measurement periods, but nonetheless, there was inverse correlation ($R^2 = 0.47$) with soil respiration (figure 20). In general, an inverse correlation is also found between soil moisture and soil temperature. This was also seen in these results, but the correlation ($R^2 = 0.34$) was not that significant. Small dataset and variation may have affected the rate of explanability.

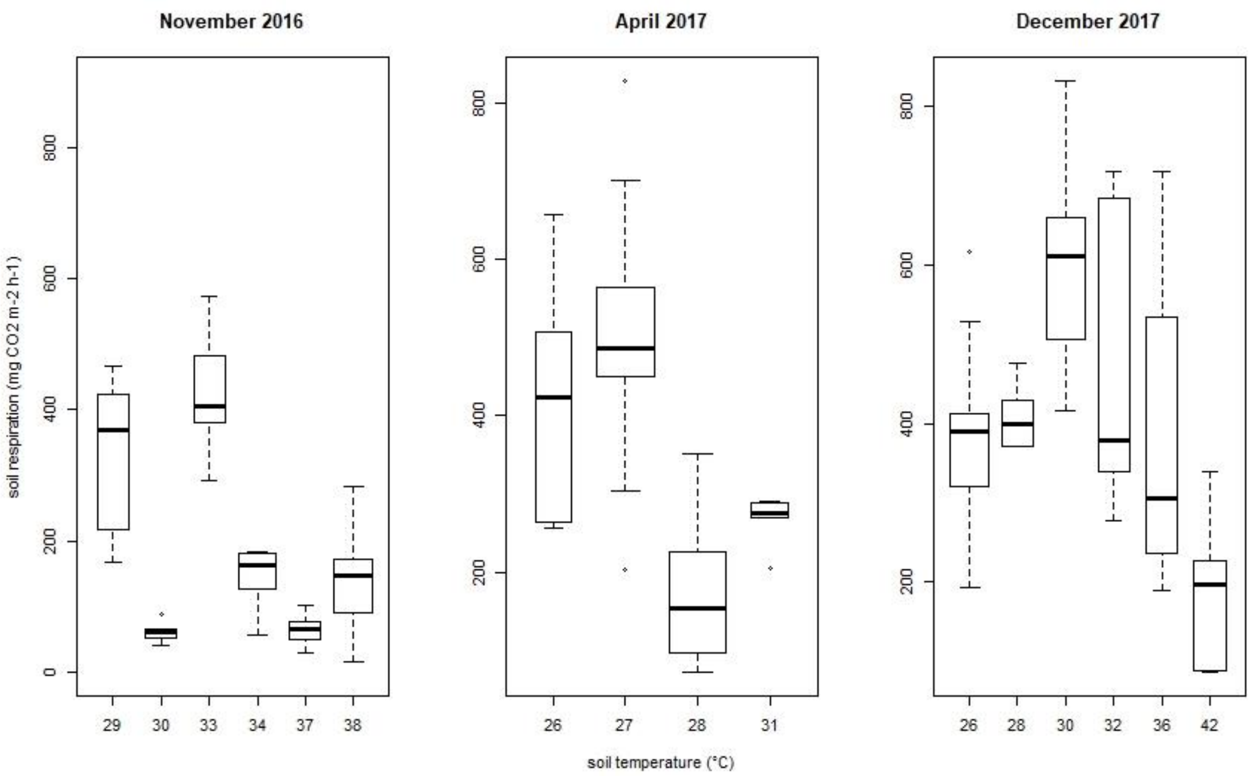

Figure 20: Relation between soil respiration and soil temperature from all mounds in all measurement periods.

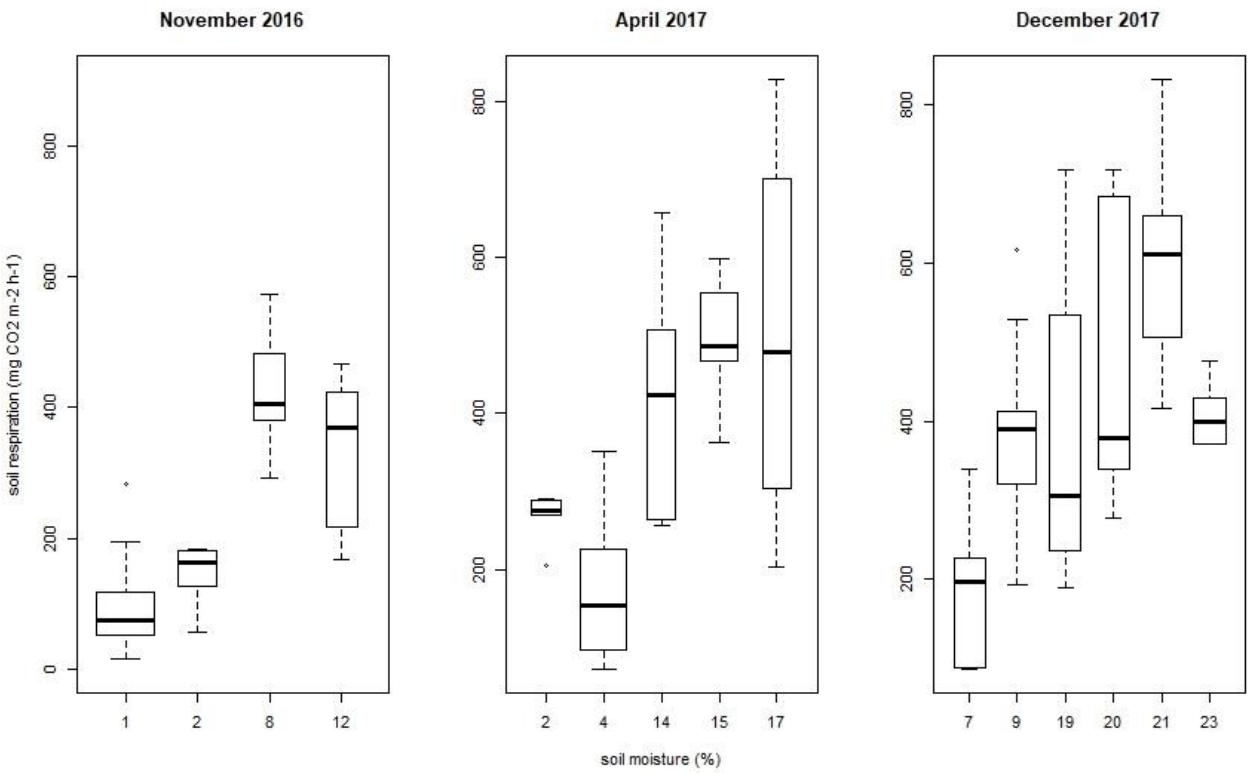

Figure 21: Relation between soil respiration and soil moisture from all mounds in all measurement periods.

Spatial factors between measurement sites was also compared. In table 2, the seasonal average respiration of savannas has been observed by calculating the average of all measured rates of soil respiration. This was separately done for the values of both measurement sites so that they can be compared. In Mbula, soil respiration rates in all seasons were lower than in Salt Lick. Spatial differences between measurement Salt Lick and Mbula sites are also likely to be explained by soil moisture and soil temperature. Mbula measurement site was drier, soil temperatures were higher, and soil respiration rates were lower in all measurement periods (table 2). Although the percentage woody vegetation cover and thereby the number of roots in Mbula was higher, this did not explain soil respiration rates. Soil respiration was more likely affected by the soil carbon content than the amount of vegetation. In Mbula, termite densities were higher and there were more active mounds, but the mounds were larger in volume in Salt Lick. The large number and small size of the mounds could indicate that the termites had a smaller foraging area in Mbula and thus the activity of termites in the soil would be lower. Mound sizes and termite biomass can also directly explain the differences between measurement sites.

Table 2: Seasonal averages of soil respiration from both measurement sites.

	November	April	December
Salt Lick	279	409	489
Mbula	94	267	323

Soil respiration was measured from 1, 2, and 10 meters from the mounds in both measurement sites (table 3). 1 and 2 meters from the mound belongs to the inner zone while the main foraging zone usually begins 10 meters from the mound. Soil respiration rates were higher in the inner zone in both measurement sites. From this it may be inferred that the activity of the termites is higher in the inner zone than in the foraging zone, that starts approximately 10 meters from the mound.

Table 3: Averages of soil respiration at different distances from the mound during the rainy season in December 2017

	1 m	2 m	10 m
Salt Lick	479	481	368
Mbula	435	324	352

6 DISCUSSION

Increasing soil respiration rates are most likely to be explained by increased soil moisture, as many of the previous studies indicate. It was therefore very clear that the effect of soil moisture was the main factor driving the changes in soil respiration rates in this study. Soil temperature also had an effect on soil respiration rates, but with little variation, it remained a smaller explanatory factor. Soil respiration rates could also be explained by seasonal changes between measurement periods, the effect of wind and mound ventilation type, and spatial differences between measurement sites.

6.1 Seasonal changes

Increased rainfall in the area explains the increase in soil moisture and soil respiration rates between measurement periods. Before measurements in November 2016, rainfall had been really low, and the soil was really dry . Rainfall increased before the measurements in April 2017 and the largest amounts of water rained before the measurements in December 2017. Higher soil respiration rates were obtained during these wet seasons in both measurement sites. Wachiye et al. (2020) reported similar results from the same measurement area. In rainy seasons termite mounds tend to have greater biomass. Due to increased soil moisture and termite biomass, the activity of termites possibly increased between measurement periods causing an increase in CO_2 emissions outside the mounds. Jamali et al. (2011) noticed that termites emit more CO_2 in wet season, and this could also be reflected in the results of this study. Because more food is available for termites, the size of their colonies may grow. Food quality and quantity can also change rates of termite metabolism, and therefore respiration rates (Jamali et al. 2011). They can also use their entire mound efficiently when it is successfully cooled by moisture evaporation (Noirot & Darlington 2000). Increased soil respiration rates between measurement periods can be estimated to be due to a change in termite activity caused by a significant increase in soil moisture.

However, soil respiration can vary considerably at different measurement points due to completely different and termite unrelated reasons. An increase in soil respiration rates during the wet season can be a result of increased root respiration due to more active plant growth. Increased activity of soil microbes and macrofauna also increases soil respiration during the rainy season (Moyano et al. 2013). The amount of root biomass or its changes between measurement seasons is not known. The moisture variability of the soil surface layer is rapid because evaporation is strong in the area. Thus, soil moisture measurements taken at one point in time may not give enough information about the actual soil moisture in the deeper soil layers. It is also probable that the variation of soil surface parameters does not affect the internal conditions of the termite mounds. Therefore, it may not be possible to deduce the effect of variation in obtained values on termite activity and thus soil respiration rates around the mounds.

Soil respiration measurements made in the vicinity of termite mounds in West Africa were close to the measurement set-up of this study and should also be compared with the results obtained. The measured savannas were humid so a direct comparison with these results is not entirely accurate either. Brümmer et al. (2009) received rates varying from 50 mg CO_2 m^{-2} h^{-1} to 300 mg CO_2 m^{-2} h^{-1} at Burkina Faso. Konaté et al. (2003) received rates from around 5 to 9 μmol CO_2 m^{-1} s^{-1} in Ivory Coast, which are significantly higher than the rates obtained in this study. Differences could be explained by measurement method and savanna conditions. Overall, the savanna soil respiration averages largely follow previous results. Rates were partly higher, but it may be inferred from this that the activity of the termites would affect soil respiration rates around the mounds.

Soil respiration rates were higher around the mounds, than 10 meters from them in wet season December 2017. This could indicate higher foraging activity during wet season. The large standard deviation of soil respiration around the mounds is explained by the fact that the rates differed across the mound, possibly due to the presence of subterranean foraging tunnels. The location of these tunnels was not known and could vary after the rains. Large soil respiration rates may indicate that there was such foraging tunnel at the measurement point. I is also possible that root respiration was significant in these points. For more accurate results, the location of these tunnels around the mound should be determined. Because the contribution of termite activity to total soil respiration remains unknown, it is possible that other characteristics of the environment around mounds affect soil respiration rates. Soil properties, such as porosity, nutrients, and moisture near the mound are shaped by termites and these may affect soil respiration rates. Thus, the effect of termites on soil respiration rates around their mounds is certain in one way or another.

6.2 Wind and mound ventilation

The effect of mound ventilation and prevailing wind direction had some effect to soil respiration rates around termite mounds. From the results of the surviving mounds it was concluded that for the open mound S5 the hypothesis was true at the distance of 2 meters, but not in the distance of 1 meter and the opposite for the closed mound S2. It is possible that the emissions of the closed and in this case small (0.15 m^3) *Macrotermes michaelseni* mound S2 can affect soil respiration rates from the distance of 1 meter, with CO_2 exiting directly from the nest trough porous wall of the mound. The nest could possibly extend underground for a distance of 1 meter. Due to internal ventilation system of open and larger (0.89 m^3) *Macrotermes subhyalinus* mound S5, CO_2 is possibly removed farther from the mound by the thrust of the wind. Unfortunately, there was too little data to examine the differences between different types of mounds in more detail.

Very few conclusions can be drawn from these results about the effect of wind or its direction to soil respiration rates around the mounds. This is at least because it is not known in which direction the mounds had ventilation passages or subterranean foraging tunnels. Also, the amounts of CO_2 inside the mound and the nest are not known, in which case it is not known how much the air leaving the mound affects soil respiration. In the nests of *Macrotermes michaelseni* the amount of CO_2 is usually higher, but its effect on these results cannot be proven. The variation was greatest in December 2017 at two meters from mound S5 at direction of 180°. The mound has probably been very active, and the wind has possibly pushed a lot of CO_2 out of it in gusts, which would explain the variation. Ocko et al. (2017) noted that wind is rarely the sole driver of internal transient flows inside the mound and is a significant contributor only on windy days and windier moments during the day. Wind speed during the measurements remains unknown. All of the mounds were measured on different days, so wind speed and gust certainly varied in measurement times, so this may have potentially affected the results and even distorted them.

6.3 Differences between measurement sites

Soil respiration rates were higher in Salt Lick during all measurement periods. The soil was also wetter and cooler, so the conditions for soil respiration were more favorable. According to study by Wachiye et al. (2020) from the same area, carbon content in bushland similar to Mbula site was 0.77 %, while it was 0.93 % in the conservation area, where Salt Lick site is located. This difference could also explain higher soil respiration rates in Salt Lick. Grasslands are noticed to emit more CO_2 compared to farmland and bushland (Brümmer et al. 2009; Wachiye et al. 2020), probably due to the better ability of their soil to bind water and the composition of their vegetation. Differences in sites could also be explained by differences in active termite mound densities: in Mbula where densities higher, colonies might have smaller territories and thus less foraging activity (Pringle & Tarnita 2017). Also, in Mbula the ratio of soil respiration rates between the mounds remained the same between measurement periods. It can possibly be assumed, that the mounds in the area were more accustomed to variations in weather conditions, and therefore the activity and number of termites in the mounds remained constant. Conclusions should not be drawn from this observation alone.

Presumably, however, the differences are mainly explained by differences in soil moisture and temperature. The increased activity of soil microbes and macrofauna and the rate of root growth in wetter conditions would explain the differences between the measurement sites. Makhado & Scholes (2011) found that soil respiration begins to decrease when the soil temperature exceeds 28°C. Soil temperatures did not fall below this, so its potential impact could not be compared. Brümmer et al. (2009) received soil respiration rates close to zero, when soil moisture was below 10 % and soil temperature over 40°C. This could explain low soil respiration rates that were measured in Mbula in November 2016. The explanability of soil moisture and soil temperature values were also in line with previous results.

Soil respiration rates measured 10 meters from the mounds (Salt Lick 368 mg CO_2 m^{-2} h^{-1}, Mbula 352 mg CO_2 m^{-2} h^{-1}) in December 2017 can be assumed to represent the average soil respiration of different types of savannas. These values can be compared to measurements of savanna soil respiration made by others. Schulze (1967) estimated total respiration from savanna soils in Costa Rica to be 300–400 mg CO_2 m^{-2} h^{-1}. Medina & Zelwer (1972) estimated total soil respiration in Venezuelan savanna to be 257–532 mg CO_2 m^{-2} h^{-1}. Makhado & Scholes (2011) estimated total soil respiration in South African savanna to be about 540 mg CO_2 m^{-2} h^{-1}. Compared to these values, the results of this study would be accurate. Deviating from these results, Wachiye et al. (2020) received significantly lower soil respiration rates from almost the same measurement sites. In conservation site near Salt Lick, rates were 75±6 mg CO_2 m^{-2} $h^{-}1$ and from bushland site, similar to Mbula, rates were 45±4 mg CO_2 m^{-2} h^{-1} as an annual average. Although the measurement method differed, it is difficult to explain the differences. Savanna types, weather conditions, and measurement methods certainly differ from study to study, so direct comparisons with other values cannot be made.

Although the mounds of *Macrotermes michaelseni* were larger and soil respiration rates around them were higher in November 2016, no significant correlations were found for mound volumes and soil respiration rates during all measurement periods. From this it can be concluded that other parameters affect soil respiration rates more than the size of the mound. It should be remembered that the volume of the mound is only an estimate obtained by calculating the above-ground parts of the mound. The subterranean part of the mound may be significantly larger, and the true size of the mound remains unknown. Also, the role of mound type on the activity of termites around it cannot be determined in this study, and other parameters affecting soil respiration are likely to be more important.

6.4 Uncertainties

As always in the study, it is good to look at possible uncertainties here as well. Potential uncertainties relate to measurements, assumptions, and analysis. Although clearly erroneous measurements were discarded, the possibility of user or device related issues cannot be ruled out. Measurement conditions were difficult and there were a long drive to the accommodation where the equipment could be maintained and charged. Under these circumstances, human error may have occurred.

Some of the made assumptions may be incorrect. Even if the termite colony have abandoned their mound, there may have be other fauna and activity in and around the mounds. The contribution of termite activity and its effect on soil respiration may be exaggerated due to the lack of precise information on their subterranean activity. It is possible that respiration from grass or tree roots, especially in Mbula measurement site contributed to the soil respiration measurements. In sampling bare soil was chosen but absence of roots were not properly checked, especially from deeper soil layers. This was especially problematic in the measurements where there was a lot of vegetation around the mound. The results were presumably more accurate in Salt Lick, where the amount of woody vegetation was lower. Thus, the proportion of different factors of soil respiration cannot be determined more precisely. Possible over-representation of emissions may also have occurred if one of the measurement points has been directly above the termite foraging tunnel. On the other hand, it was the point of this study, as large amounts of soil respiration may indicate termites and their activity in soil.

Mounds were measured on different days, so weather conditions may have changed between measurements. Mounds were measured between 10 a.m. and 4 p.m., due to their remote location. Their diurnal cycle of mounds may therefore have been at different stages with different measurement days, and this may have affected the results. However, diurnal variation in soil respiration rates is usually small, and the variation is more affected by changes in soil moisture and soil temperature. Analysis can also cause some issues, for example distortion and errors are unfortunately typical when analyzing data. Also, long time between measurements and analysis can affect the results, no matter how reliable the documentation was. Pumpanen et al. (2004) stated that static closed chamber method seem to underestimate CO_2 fluxes by 10–35 %, so in reality, soil respiration rates may have been even higher.

6.5 Further research

Research on this topic should be deepened with regard to uncertainties. The most important would be to get more information about the activity of termites in the soil and to figure out the true size of the subterranean part of the mound. It would also be important to find a way to determine the actual size of the whole mound without breaking them down. One possibility is to use ground-penetrating radar technique. By estimating the size and volume of the mound, conclusions can be drawn about the termite biomass. The exact location of subterranean fungus galleries and the nest can also be detected using this technique, and thus their effect on soil respiration can be refined. The radar would also provide a more accurate view of the foraging tunnel network outside the mound, and the theory of the effect of termite activity to soil respiration around the mound could be better tested.

Soil respiration measurements could have been taken from an even longer distance from the mound. The problem here could be termites from other termite mounds. When the size of the foraging zone for a particular mound cannot be determined, the activity of the termites farther from the mound may be influenced by another termite colony from another mound. Then the results would presumably correspond to the average savanna soil respiration. The activity of termites around particular mound could be studied by measuring a transect leaving from the mound. Measurement points could be every meter and the transect could extend up to 30 meters from the mound. This could be successful, for example, in Salt Lick site where there are fewer active termite mounds and their areas of influence would not collide as easily. This would provide information about changes in soil respiration rates in the vicinity of the mound.

To refine the results, parameters such as soil temperature and soil moisture should be measured continuously during the measurements. In this way, changes in instantaneous measurement conditions, such as the effects of individual rainfall, would not be highlighted in the study. Also, if the effect of wind is to be studied in more detail, the instantaneous wind speeds should be measured. Ground-penetrating radar technique could also be applied to detect the amount of water inside the mound, in which case the effect of moisture on the activity of the termites could be determined more accurately.

Other parameters of the mound environment could be studied by taking soil samples from the soils around the mound. Samples could be used to study soil composition and to determine soil porosity, nutrients and the soil carbon content. These could be used to further interpret the differences between the mounds and explain the obtained soil respiration rates. The contribution of termite emissions to total soil respiration is not known, so studying it could refine the results. In any case, research on this topic should be deepened. In this study, estimates of the correlation between termite activity and soil respiration are only indicative. The contribution of other parameters such as wind, soil moisture and soil temperature to changes in soil respiration rates should also be specified in some way.

7 CONCLUSIONS

In conclusion, a single reason for the changes in soil respiration rates around termite mounds is difficult to find. Soil respiration rates were most affected by soil moisture and soil temperature, as expected from the existing research. Also, the differences between the measurement sites were mainly explained by the variation of these two parameters, and differences in soil carbon content. Although the mounds were larger in Salt Lick, the size of the mound or the type of the termite species inhabiting them did not affect the results. The assumption is that the size of the mound would have had a greater effect on soil respiration rates around it if accurate information on the actual size of the mound would have been available. Ventilation inside the mound is likely to affect CO2 emissions at least somehow outside the mound as well. The prevailing wind direction would thus affect the rates of soil respiration around the mound. Although the ventilation inside the mounds of these two termite species is different, so the effect of these differences to soil respiration rates cannot be properly observed in this study, due to the limited amount of data. The most important characteristic of arid and semi-arid savannas, in particular, is the seasonal variation of rainfall. The study showed that this also affects soil respiration: during the rainy season, soil respiration rates were significantly higher, partly due to possibly increased termite activity. In the vicinity of the termite mounds (in distance of 1 and 2 meters) at the inner zone, respiration values were higher than in the termite foraging zone 10 meters from the mound. It can possibly be assumed that the differences are due either to the activity of the termites around the mounds or to the effect of the termites on the soil properties near the mounds.

Thus, with some reservations, it can be stated that soil respiration around the mounds is likely to be affected by both termite activity and the prevailing wind direction. Of the other parameters, soil respiration was most affected by soil moisture and soil temperature. There are still many uncertainties on the subject and research should thus be expanded.

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